Effects of species' body mass, diversity and phenology on complex food-web stability

Vom Fachbereich Biologie der Technischen Universität Darmstadt
zur Erlangung des akademischen Grades eines
Doctor rerum naturalium genehmigte Dissertation von

Dipl.-Biol. Sonja B. Otto
aus Nürnberg.

Referenten:
Dr. Ulrich Brose
Prof. Dr. Stefan Scheu

Eingereicht am 25. Januar 2008
Mündliche Prüfung am 15. April 2008
Darmstadt 2008 – D 17

TECHNISCHE UNIVERSITÄT DARMSTADT

Die vorliegende Arbeit wurde in der Arbeitsgruppe von Dr. Ulrich Brose zwischen Oktober 2004 und Januar 2008 angefertigt.

Meiner Familie

List of peer-reviewed publications in this thesis

Chapter 2

Otto, S.B., Berlow, E.L., Rank, N.E., Smiley, J. & Brose, U. (2008). The diversity and identity of predators drive interaction strengths and trophic cascades in a montane food web. *Ecology*(89) 1.

Chapter 3

Otto, S.B., Rall, B.C. & Brose, U. (2007). Allometric degree distributions facilitate food web stability. *Nature*(450)1: 1226-1229.

Prospective submission early in 2008

Chapter 4

Otto, S.B., Martinez, N.D. & Brose, U. (2008). Body mass and network structure drive food-web robustness against secondary extinctions.

Chapter 5

Brose, U., Banašek-Richter, C., **Otto, S.B.**, Rall, B.C., Martinez, N.D. & Dunne, J. (2008). The complexity, topology and diversity of food webs.

Table of Contents

Chapter 1

General Introduction

Picture of a guava plant that M.S. Merian drew in Surinam, South America, in 1705. Merian gives a detailed description of the feeding interactions of two herbivores on a plant, the caterpillar of a deltoid moth (Fam. Noctuidae) and a species she described as "the green caterpillar" on top of the leaves. For the latter, Merian also described parasitoid infestation and was probably the first person having described and (almost) pictured a tri-trophic food chain.

1.1 Aim and Scope

The aim of my studies was to gain knowledge of the complex interrelationships between the species in natural ecosystems. This knowledge is the first step on a long way to understand how the multifaceted dynamics between individual species may affect a whole community. This thesis addresses a broad scope of ecological relevant questions and domains, and focuses mainly on the foundations of the co-existence of species, the interactions between them, and the effects of species loss. It combines projects that acquired data by empirical field research, with those using modern technologies such as theoretical simulations. This includes the processing of empirical data with the help of theoretical modelling, which is an important instrument to predict and at the same time to explain what might happen to natural communities after perturbations. The four projects presented here all address the analyses of empirical food-web data regarding the stability of natural communities under different aspects.

1.2 What food webs are

Natural ecosystems exhibit striking species richness. It puzzled natural scientists since the early beginnings of the discipline, how species interact, depend on each other, and how their overwhelming diversity is maintained (e.g., Darwin 1859, Elton 1927, MacArthur 1957, Hutchinson 1959; to list just a few of the most influential names). The interrelationships between species that co-exist in an ecosystem comprise a large range of interactions, such as the pollination of plants by insects, the provision of shelter or the fight for territory. However, these non-trophic interactions are difficult to include when drawing the picture of a complex species' community. Thus, common descriptors of food webs are species' trophic interactions, that is who eats whom, and if possible, in which amount. This was prominently summarized already by Hutchinson in 1959, who stated:

> "*Food relations appear as one of the most important aspects of the system of animate nature. There is quite obviously much more to living communities than the raw dictum "eat or be eaten", but in order to understand the higher intricacies of any ecological system, it is most easy to start from this crudely simple point of view.*" (Hutchinson 1959, p. 147).

Food webs represent ecological communities of species that are interlinked by feeding interactions. Consumer-resource pairs of two species describe the most simple bi-trophic food-web motif. The interlinking of many bi-, tri- and multi-trophic food-web motifs leads to a complex three-dimensional network of connected species. Direct trophic interactions within food webs illustrate how the flux of energy is transferred between species' populations by consuming and being consumed and how species depend on each other. Furthermore, the direct interaction between two species may result in indirect effects on other species. This idea of dynamic processes between the species helps to understand why perturbations of one interaction in a food web might trigger cascading effects on others.

Food webs and food-web motifs, and therein mainly the dynamics between the interacting species, gained increasing attention during the last century. Seminal in this context are the prominent models on predator-prey dynamics of Alfred Lotka, Vivo Volterra and Rosenzweig and MacArthur (Lotka 1925, Volterra 1926, Rosenzweig & MacArthur 1963). Charles Elton was a pioneer on the study of animal interactions in food-chains and understood them as an important part of the complex relationships in natural communities (Elton 1927). Robert MacArthur pushed the development of theoretical ecology forward. He was among the first, who introduced mathematical models to describe and test methods on community processes, such as the frequency distribution of species (MacArthur 1957) or the dynamical division of ecological niches (MacArthur 1958). Later, Hairston and co-workers (Hairston *et al.* 1960) summarized the implications of top-down pressure, executed by predatory species on their prey, as well as bottom-up forces, exerted by low trophic levels on higher ones in food chains. They introduced the famous concept of a "green world", stating that resource limitation depends on the trophic position of a species in a food chain. They argue that top-down forces from predators to herbivores may release plants from consumption, an energetic concept that implies that higher trophic levels that are not regulated by predation themselves and low trophic levels that are released from regulation by herbivores, might be controlled by competition. These early concepts of niche separation, species' distributions and dynamical processes between the species are still from major importance in modern ecology.

Beside simple predator-prey interactions, one of the most intensively studied motifs is the tri-trophic food chain. Studies on three-species food chains deepened the understanding of energetic interactions between species (e.g., Jonsson & Ebenman 1998) and expanded the understanding of "stability" by evaluating for example the possibility of persistent chaotic dynamics (Hastings & Powell 1991, McCann & Yodzis 1994). The simple tri-trophic motif was and still is an important object to study in order

to understand complex patterns such as energy transfer over more than one link in a network (e.g., Bascompte & Melián 2005). Chapter 2 of this work presents cascading effects of species loss within an empirical food web that was observed under field conditions. The study suggests strong effects if the moderately diverse food web, represented by three predators preying on one prey, was reduced to simple food chains due to predator exclusion. The diversity and identity of the predators had a profound impact on prey and plant biomass. Particularly the theoretical modelling of food chains, later more complex food-web motifs such as omnivory (McCann *et al.* 1998, Fussmann & Heber 2002, Emmerson & Yearsley 2004, Vandermeer 2006) and only recently of entire food webs (Polis 1998, Williams & Martinez 2000, 2004a, b, Brose *et al.* 2005b) is an essential instrument to comprehend species' interactions. Chapter 3 of this thesis uses computational simulations of tri-trophic food chains that yield interesting mechanistic predictions concerning the stability of entire natural ecosystems.

The sampling, description and illustration of food webs are both traditional and modern at the same time. The first images of bi-trophic herbivore-plant interactions are probably represented in the work of Maria Sibylla Merian since 1679 (see Merian 1679, 1705 and cover picture). The more scientific notion of species communities was started in 1887 by Stephen Forbes (Forbes 1887), who described an entire lake food web in great detail. The trend to describe large food webs in increasingly detailed resolution was carried forward in the 1910s (Pierce *et al.* 1912, Shelford 1913) and 1920s (Summerhayes & Elton 1923, 1928; Elton 1927) until today. In 1958, Elton was the first to present a collection of quantitative representations of 30 food webs, describing their species and feeding interactions as precise as possible (Elton 1958). This induced the sampling of contemporary food webs with a high taxonomic resolution [e.g., Skipwith Pond (Warren 1989), Coachella Dessert (Polis 1991), Little Rock Lake (Martinez 1991) or Weddell Sea (Ute Jacobs, unpublished)] and built the cornerstone of the assemblage of modern food-web databases (Cohen 1989, Sutherland 1989, Brose *et al.* 2005b).

However, to provide a general introduction on what food webs are, it is similarly important to give a short insight in the flaws of the current data. It is very difficult to achieve the desired high taxonomic resolution of all different species and it is even more difficult to map the entire complexity (in terms of every single link for every species) of a real-life food web. The feeding links are achieved by observations mainly, whereas this is difficult if not impossible for small insects and aquatic or below-ground ecosystems. Feeding trials in the laboratory, literature research and expert estimates on energy fluxes (Hunt *et al.* 1987) give reasonable but still insufficient hints on

possible feeding interactions. Manual gut analyses (e.g., Winemiller 1989, 1990, Woodward & Hildrew 2001) or modern DNA-based multiplex analyses of gut contents (e.g., Sheppard *et al.* 2005) are promising but are inadequate for species with extra-intestinal digestion, for example spiders and chilopods. Therefore, in many food-web descriptions, groups of species that share approximate size and diet are aggregated as "trophic species" and are treated similar to actual biological species. These trophically related groups of species can span whole kingdoms (e.g., mites, fungi) or mixed groups of similar individuals (e.g., phytoplankton, zooplankton, "Nematodes"). Further simplifications of food-web descriptions occur as different life stages of species, which are very likely to differ in diet, are mostly ignored. Modern food webs also include non-living organic matter, i.e., detritus as a species, which is recognized as an important energy resource for ecosystems. This is on one hand positively to note, as the inclusion of detritus in model food webs allows for naturally more reasonable analyses and predictions. On the other hand, if the body masses of the species in food webs are to be included in the descriptions, the modelling of detritus, or similarly of plants, yields difficulties.

This brief listing shows that ecological networks are amazingly complex formations of often remarkable diversity. Even modern food-web data, achieved by applying exhaustive sampling efforts, is restricted to represent nature as just a sketch or as an "educated best guess". However, food webs serve well to demonstrate how fragile ecosystems are and how their persistence is dependent on various parameters. With the help of food webs mankind may learn, that only minor perturbations in these parameters can lead to significant changes in network structure and the composition of species communities.

1.3 Food-web stability

Facing the seventh wave of species' mass extinction, one of the largest and fastest epochs of species losses ever (Pimm *et al.* 1995, Hughes *et al.* 1997, Salà *et al.* 2000), science is increasingly challenged to analyse the different aspects of food-web stability. The term "stability" has been variously defined to describe population or system equilibrium, persistence, robustness, and resilience (definitions given in McCann 2000). In some cases stability refers to the outcome of internal dynamics (intrinsic stability) while in other cases it reflects the response of a population or system to a perturbation such as species loss (perturbation stability). Most of the work presented here focuses on perturbation stability and the persistence of food-webs. Persistence is defined as the fraction of species that endures after perturbations compared to the initial number

of species in the system before perturbation.

1.3.1 The Diversity – Stability Debate

The persistence of a food web is dependent on a large variety of parameters that have been studied, elucidated and explained during the last decades. Early studies started to analyse the dependence of food-web stability on species diversity (Elton 1933, Odum 1953, MacArthur 1955, Elton 1958). They established an enduring dominant paradigm, that food webs with high species diversity, resulting in increased complexity, are more stable than species-poor food webs. They argued, that the higher the number of "energetic pathways" per species was (i.e., the more links a species had), the better the control of population size (MacArthur 1955) and the higher the compensatory capacity of the food webs in case of species loss. This paradigm, derived from observational studies of empirical networks, was challenged by early theoretical studies (Gardner & Ashby 1970, May 1972, 1973). Applying mathematical simulation methods, these studies analyzed the dynamical behaviour of theoretical networks with varying species diversity. The results claim that randomly assembled complex networks of high diversity are less stable than simple networks. This contradiction led to a long lasting scientific debate, addressing the diversity-stability problem (see McCann 2000, Montoya *et al.* 2006 for reviews).

The discussion on the stability of natural food webs is still in progress in modern ecology. It gave an impulse to investigate the stability of food webs under a variety of different parameters. The main criticism on the early theoretical models was and is their lack of reasonable biological assumptions. Improving mathematical models in this direction lead to the suggestion that there might in deed be a positive diversity-stability relation (De Angelis 1975). For a long time, De Angelis' study was the only theoretical work that confirmed the empirical observations. Pimm and Lawton (Pimm & Lawton 1977, Pimm 1979) corroborated the theoretical proclamations that high-diversity food webs are less stable than species-poor ones, in suggesting that stability decreases with an increasing number of trophic levels. This confirmed earlier studies (MacArthur 1955) and established the fact that the number of trophic levels in a food web can serve as an indirect measure of species diversity as larger food webs are more likely to build higher trophic levels than small ones (Post *et al.* 2000b). Subsequent theoretical work focused on the valuation of random network models used by May (May 1972), and compared random network properties to those of natural food webs. The studies found that the link structure of natural networks is more capable to stabilize persistent populations than random ones (Yodzis 1981), and that empirical patterns of interactions between the species generate higher local stability than randomly assembled community matrices (De Ruiter *et al.* 1995, Neutel *et al.* 2002). This was an

apparent rejection of Mays arguments, that the evaluation of random food-web structures might help to explain stability (May 1972), and clearly states that random network structures do not resemble empirical ones (Lawlor 1978, see also Williams & Martinez 2000, Dunne *et al.* 2002, 2004).

Further possible parameters that may affect the stability of natural food webs have been analyzed recently. Besides the strength of direct interaction between two species (Berlow 1999, Berlow *et al.* 2004), it is of increasing interest to describe the "functional response", the feeding pattern between consumers and their resources in more biological detail. The amount of prey intake has been recognized to depend on prey density (Holling 1959a, b) and interference between the predatory species (Beddington 1975, De Angelis *et al.* 1975). This is different from earlier simplifications, that describe a linear dependency, where the predator eats more the more prey is available, without any saturation (Lotka 1925, Volterra 1926). Despite being criticised to be biologically unrealistic – though the linear predator-prey functional response might adequately describe filter feeders and scavengers (Jeschke *et al.* 2004) and is thus very specific – this model assumption is still largely applied in theoretical modelling today. Biologically more reasonable (Jeschke *et al.* 2004) is the use of *Hollings Type II* functional response (Holling 1959a, b) that describes the increase of the feeding capacity of a predator with increasing prey density up to a saturating limit which indicates the maximum ingestion rate of a predator. It is thus used in the studies presented in Chapters 3 and 4 of this work, where the simulation of bioenergetic dynamics of species from natural food webs give interesting insights in food-web stability in general (Chapter 3) and after species loss (Chapter 4). *Hollings Type III* functional response describes sigmoid feeding dependencies, indicating that species can escape predation at very low densities or because they found shelter. *Type III* and hump-shaped predator-interference functional responses were found to stabilize food webs and population persistence more than *Type II* (Williams & Martinez 2004b, Rall *et al.* 2008) and can be easily understood to represent biological conditions in real-world ecosystems. However, to predict consequences of community perturbations they are mostly inappropriate, as the intrinsic stability per se due to *Type III* or predator-interference functional responses might coat destabilizing impacts. Also dependent on prey density, the aspect of predator switching between different prey due to their availability was thoroughly analyzed (Post *et al.* 2000a, Brose *et al.* 2003, Kondoh 2003). This "adaptive foraging" changes the strength of links depending on the relative abundances of the prey and is such a dynamic mechanism to shift energy fluxes between the species, which might influence the stability in complex communities (Kondoh 2003).

Concomitant to the research on more complex food-web motifs is the notion that omnivory, that is if species feed on several trophic levels sometimes including their own, can stabilize population persistence under certain assumptions (e.g., McCann & Hastings 1997, Vandermeer 2006). The linking of species, describing the local structure of species within the three dimensional food webs, ought to open an entirely new field of stability research. The structure of food webs *per se* has profound implications on food web stability (Dunne 2006, Martinez *et al.* 2006) and is discussed in greater detail in Chapters 1.4. and 4.

1.3.2 Implications of body mass

It is only in recent years that ecologists comprehend the importance of the body masses of species in empirical food webs to have a considerable effect on the stability of whole ecosystems. This late awareness is astonishing, as the strong relationship between species' size and species' metabolism is well and long known (Kleiber 1932, 1947). Live depends on energy, and the energy gain of living creatures is achieved either by autotrophic nutrient conversion by plant species or by feeding on energy rich sources, namely plants or other animals. It's the energy flux from low trophic levels up to higher ones that maintains the striking species richness in natural ecosystems. This is warranted via the uptake, conversion and procession of nutrients within individual species. It is thus not unexpected that the body masses of species play an important role in whole ecosystem persistence.

The "Metabolic Theory of Ecology" (Brown *et al.* 2004) represents an essential model on how and why species' respiration may depend on species' size (West *et al.* 1997, 1999; Enquist *et al.* 1999, Gillooly *et al.* 2001, Savage *et al.* 2004b). Despite recent challenges of the metabolic theory (Makarieva *et al.* 2005a, b), it is a common perception, that metabolism scales with body mass with a power-law with an exponent of 0.75 ("Kleibers law", Kleiber 1932, 1947, 1961). This value is mechanistically explained by the assumption, that all living creatures share a fractal-like network to transport nutrients, such as the capillary system in mammals, tracheas in insects or plants vascular system (West *et al.* 1997). The three-quarter exponent is consistently challenged by a second theory, stating that metabolism scales with the surface of the respiratory organs in organisms (Rubner 1883). Together with Euclidean Geometry, which defines the dependence between surface and volume of a body (i.e., species size), this theory yields an exponent of 0.66 of metabolism with body mass. However, as quarter-exponents scaling with body masses, such as the circulation of the blood volume or the growth time of organisms, were known phenomena in ecology (reviewed in Lindstedt & Calder 1981), Kleibers law is more broadly accepted, and therefore implemented in most recent theoretical models on bioenergetic population

dynamics (e.g., McCann & Yodzis 1994, McCann *et al.* 1998, Brose *et al.* 2006, Chapters 3 and 4 in this work). An interesting comparison of the two different metabolic theories is given by Van der Meer (2006). Normalizing the quarter-power metabolism per unit biomass of the individuals yields a negative one quarter-power law of respiration to body mass (Yodzis & Innes 1992). This means that large animals expend more total energy than small ones, but spend relatively much less energy per unit biomass to maintain life. Thus, increasing species' size decreases its relative rates of metabolism and consumption (Yodzis & Innes 1992), and causes implications on individual growth (Enquist *et al.* 1999, Brown *et al.* 2004), and the development of the species (Brown *et al.* 2004). The assimilation efficiency describes the fraction of energy that is transformed to maintain the organism and to build up biomass, either by individual growth or by reproduction (i.e., population biomass). Large parts of the consumed nutrients are circled back to the ecosystem by faeces loss, for example 15% in case of carnivores and 45% in case of herbivores (Yodzis & Innes 1992).

In 1992, Yodzis and Innes (Yodzis & Innes 1992) were precursors in describing predator-prey dynamics in a body-mass based model that considers the bioenergetic dynamics between species due to metabolic principles. The model has been refined with empirically achieved allometric constants (Enquist *et al.* 1999, Brown *et al.* 2004), i.e., constants that incorporate differences in metabolic taxa, such as invertebrate, ectotherm and endotherm vertebrate species, and is able to calculate the bioenergetic dynamics in biologically reasonable detail. Recent work updated the simple predator-prey model to bioenergetic models of complex food webs (Brose *et al.* 2003, Williams & Martinez 2004a). On the basis of the new allometric and dynamic model (Yodzis & Innes 1992), recent analyses on food-chain stability integrated body-size dependent Lotka-Volterra dynamics (Yodzis & Innes 1992, Jonsson & Ebenman 1998, Emmerson & Raffaelli 2004). The food web of Ythan Estuary in northern Scotland was among the first natural networks where body-mass data of the species was sampled besides the linking information. Its investigation revealed a strong relationship between the interaction strengths and the body size of the interacting species. Associated theoretical simulations based on the empirically sampled food-web data showed that the strength of this body size-interaction strength relationship was crucial for the stability of entire food webs (Emmerson & Raffaelli 2004). Subsequent studies concerning body mass and stability supported the new assumption, and showed that the body-mass ratios between predators and prey species affect whole system stability (Brose *et al.* 2006). Chapter 3 in this thesis addresses the implications of empirical body-mass distributions within food webs. Captivatingly, we found a strong relationship of the local link structure of species with their body mass and resultant effects on food-web stability. Interestingly, theoretical simulations of Brose *et al.* (2006) found that

population persistence in complex food webs decreases with increasing species diversity (corroborating classical theoretical assumptions, e.g., May 1972) but only if the assumed average predator size is smaller or up to tenfold larger than its average prey size (Brose *et al.* 2006). However, the empirical body-mass distribution of species in food webs leads to average body-mass ratios larger than 10 (Brose *et al.* 2006). Thus, increasing the simulated average body-mass ratios yielded the opposite result, namely the increase of population persistence with increasing food-web diversity (Brose *et al.* 2006). This study corroborates early empirical findings in the diversity-stability conundrum. Further work on body-mass related effects associated with biologically realistic population dynamics (i.e., based on metabolism) in complex networks promises fundamental insights in food-web functioning (see for example, Savage *et al.* 2004a, Weitz & Levin 2006).

1.4 Food-web structure

As already addressed in the previous chapter, the structure of food webs is particularly relevant for ecosystem functioning and the stability of natural food webs. Food-web structure, or synonymously food-web topology, is determined by species' interactions. The number of links between species and more precise the number of ingoing and outgoing links (that is, the number of predators and prey) of one species determines the local link structure within food webs. All links together are interwoven to build a complex, three-dimensional food-web entity. The interlinking within these complex networks builds the foundation for pathways of energy flux and is thus the key to understand food-web dynamics. The elucidation of general structural patterns of natural ecosystems may further reveal universal principles of the organisation of species' communities. This was the goal of scientists throughout the last decades (e.g., Cohen 1978).

Three established measures of bio-complexity, which are important in order to compare networks among each other, are the number of feeding interactions (L), the number of links per species (L/S, where S is the number of species in the network) and food-web connectance (i.e., the proportion of realized links within the food webs, calculated as the number of actual links divided by the squared number of species, which gives the number of possible links within a network; Martinez 1991). It is a long standing debate, whether food-web connectance declines with species diversity, which would keep the product of connectance and species number constant and ensure mathematically reputable stability in large food webs (May 1973). And in deed, an early empirical study that analysed 64 food webs with low species number found that

connectance decreased exponentially with increasing diversity and corroborated the theoretic assumption (Cohen & Briand 1984). As a nominal value of connectance it was suggested that species had in average 1.9 interactions, and that the link number increases with increasing diversity ("link-species scaling law", Cohen & Newman 1985). Opposing such results, Martinez (1992) analysed a set of 175 new and modern food webs that included webs with higher species diversity up to 93 species. He proposed that connectance was constant across all food webs, regardless of their size (Martinez 1992). This new and somewhat startling finding was challenged in other studies that investigated other modern food-web assemblages (Havens 1992), but was further fortified by Martinez in two subsequent studies (Martinez 1993, 1994). It is important to point out that such contrasting results in terms of connectance might be strongly influenced by the sampling effort of new and old, respectively small and large food webs (Bersier *et al.* 1999, Martinez *et al.* 1999). Thus, the dependence between biodiversity and link density in older food webs, supposedly sampled with less effort, may corroborate scale-variance. However, modern food webs were and still are achieved under the application of new techniques (e.g., Winemiller 1989, 1990), thus include more links and therewith confirm "constant connectance". Chapter 5 of this thesis deals with the implications of scale-variance vs. scale-invariance of food-web connectance in more detail. It gives a short review over the history of approved diversity-stability relationships, discusses their implications and evaluates modern high quality food-web data.

Despite the extensive presentation in Chapter 5, I will here briefly introduce some of the commonly used measures of food-web topology in order to give at least a short overview. Important food-web properties besides the scale invariant food-web patterns discussed above, are *species scaling laws* (Briand & Cohen 1984), which describe the fractions of top predators (species with no predators), intermediate species (species with both predator and prey) and basal species (mostly autotroph species with no prey), and *link scaling laws* (Cohen & Briand 1984), which express constant proportions of links between these in such way classified species. Further measures of structure include for example the average and maximum chain length within food webs (e.g., Williams *et al.* 2002), the length and weight of loops (Neutel *et al.* 2002), the amount of generality and vulnerability of species, their connectedness or link distribution (Montoya & Solé 2003). A broad and exhaustive review on food-web structure and its measures is given by Dunne (2006). Recent studies went beyond the introduced easy-to-comprehend species structural traits, and found interesting effects of the local link structure of one degree and two degree neighbours of the target species (Brose *et al.* 2005a). Very important to gather a complete picture is the inclusion of a-biotic factors on food-web structure, such as temperature (Rall *et al.*

2008) and habitat size (Hutchinson 1959; see also Brose *et al.* 2004 and references therein).

Summarizing, there exists a variety of little screws to manipulate food-web structure and to investigate their effects on food-web stability. The quest for universal constants is yet not sated, instead, the common contemporary perception is that they are unlikely to exist in natural ecosystems (see Chapter 5). The next generation of food webs, yet to be conducted, may shed light on still open questions concerning community ecology. They ought to provide new data, such as quantitative information about the link strengths between the species (in contrast to recent food webs, which provide a qualitatively excellent but only binary resolution that merely counts the links and connects the species). First theoretical approaches already deal with the question of link weight in food-web motifs (McCann *et al.* 1998, Neutel *et al.* 2002), and try to estimate relative energy fluxes due to species' abundance and body sizes in an empirical food web (Tuesday Lakes, Reuman & Cohen 2005).

1.4.1 Theoretical food-web models

Seeking to model natural food webs as realistically as possible generated a variety of stochastic models on predator-prey interaction structure. They have in common that they are based on algorithms that arrange a specific number of links among a specific number of species based on species richness and connectance as input parameters. Their predictions on food-web structures have been successfully tested against empirical data (Williams & Martinez 2000, Cattin *et al.* 2004, Stouffer *et al.* 2005). It is completive to an introduction to food-web structure, to conclude with a short presentation of the main characteristics of the four commonly used food-web models:

(a) random model (Erdös & Rényi 1960, May 1972)

The first model that has to be named in this context is the random model. It is based on the mathematical assumption that all links within networks have the same probability, that all interaction strengths between the species are equal and all kinds of distributions within the networks follow random patterns. However, in terms of biological reasonable dynamics, they oversimplify natural conditions. It was frequently shown that empirical patterns are significantly different from random ones (Yodzis 1981, Warren & Lawton 1987, De Ruiter *et al.* 1995, Neutel *et al.* 2002).

(b) cascade model (Cohen & Newman 1985)

In a series of publications on the "Stochastic Theory of Community food webs", Cohen and colleagues proposed the cascade model. It was the first model that incorporated simple rules on natural food-web structures that assign the links between

predator and possible prey species: 1. all species are arranged on a one-dimensional niche axis that ranges from zero to one, where each species is assigned with a random niche value. 2. Each species is allowed to feed on prey with lower niche values than their own. This routine of cascading interactions from upper to lower trophic levels excludes cannibalistic feeding and loops. 3. The links between the species are assigned with a random probability $p = 2CS / (S-1)$, however are restricted to the upper triangle of the feeding matrix ["upper triangularity"; the term is derived from the common notion of food webs as two dimensional feeding matrices, where links are assigned as an entry in the square that combines predatory species (in the columns of the matrices) with prey species (in the rows of the matrices)]. The algorithm assumes a constant ratio of links per species, as suggested by early theory and data. Common criticism on the cascade model is the exclusion of cannibalism, loops and lower triangular species' interactions, as all these scenarios commonly exist in natural food webs (e.g., Fox 1975, Memmott *et al.* 2000, Neutel *et al.* 2002). However, the cascade model is remarkably successful in predicting structural parameters comparable to empirical networks (Cohen *et al.* 1986, Warren & Lawton 1987) and was the first to provide evidence that non-random patterns can result in good structural predictions on complex food webs. Stouffer (2005) introduced a "generalized cascade model", where each predator may select their prey also at random, but instead of from the entire resource axis, the selections are restricted to only those species with niche values less than or equal to their own and are derived from an exponential β-distribution (where $\beta = [(\text{number of species})^2/2(\text{the number of links})]$ (Stouffer *et al.* 2005).

(c) niche model (Williams & Martinez 2000)

Similar to the cascade model, the niche model applies a one dimensional niche axis and assigns random niche values, n, between zero and one to the species on the axis. Each species may be linked (i.e., can feed) to a certain range of other species, r, which is randomly defined by a β-distribution function. The center of the feeding range, c, is drawn uniformly from the interval ($r/2 < c \leq n$) which keeps it at a lower niche value than that of the feeding species. Exceeding the approach of the cascade model, the feeding range can thus overlap and even go beyond the niche value of the target species, allowing cannibalism and loops. The algorithm assumes a constant connectance, as suggested by earlier findings of the authors (Martinez 1992). A critical aspect of the niche model is the strict continuity in the feeding axis which allows no gaps. Similar to the cascade model, Stouffer (2006) introduced a "generalized niche model" to test for the existence of gaps in the one-dimensional feeding axis of predators ("intervality", Stouffer *et al.* 2006). Surprisingly their study suggests that empirical food webs actually do show prey intervality (i.e., few gaps) which accredits

the algorithm of the niche model.

(d) nested-hierarchy model (Cattin *et al.* 2004)

Following the cascade and niche models, the nested-hierarchy model assigns random niche values between zero and one to the species on an axis. To describe the underlying rules simplified: the links per species are sampled from a β-distribution. Thereafter, species that share similar feeding ranges are grouped. Links between predators and prey are selected randomly and compared with the links within the groups. If a species has less prey items than comparable species, it randomly gets more links to prey items shared with species in the group. If more links are needed, they are assigned randomly, first with the condition that the prey has a lower, then a higher niche value than the target species. This algorithm allows gaps in the feeding ranges, loops and lower triangular feeding.

1.5 References

Bascompte J. & Melián C.J. (2005) Simple trophic modules for complex food webs. *Ecology*, 86, 2868-2873

Beddington J.R. (1975) Mutual interference between parasites or predators and its effect on searching efficiency. *Journal of Animal Ecology*, 44, 331-340

Berlow E.L. (1999) Strong effects of weak interactions in ecological communities. *Nature*, 398, 330-334

Berlow E.L., Neutel A.M., Cohen J.E., de Ruiter P.C., Ebenman B., Emmerson M., Fox J.W., Jansen V.A.A., Jones J.I., Kokkoris G.D., Logofet D.O., McKane A.J., Montoya J.M. & Petchey O. (2004) Interaction strengths in food webs: issues and opportunities. *Journal of Animal Ecology*, 73, 585-598

Bersier L.F., Dixon P. & Sugihara G. (1999) Scale-invariant or scale-dependent behavior of the link density property in food webs: a matter of sampling effort? *American Naturalist*, 153, 676-682

Briand F. & Cohen J.E. (1984) Community Food Webs Have Scale-Invariant Structure. *Nature*, 307, 264-267

Brose U., Berlow E.L. & Martinez N.D. (2005a) Scaling up keystone effects from simple to complex ecological networks. *Ecology Letters*, 8, 1317-1325

Brose U., Cushing L., Berlow E.L., Jonsson T., Banašek-Richter C., Bersier L.F., Blanchard J.L., Brey T., Carpenter S.R., Cattin Blandenier M.-F., Cohen J.E., Dawah H.A., Dell T., Edwards F., Harper-Smith S., Jacob U., Knapp R.A., Ledger M.E., Memmott J., Mintenbeck K., Pinnegar J.K., Rall B.C., Rayner T., Ruess L., Ulrich W., Warren P., Williams R.J., Woodward G., Yodzis P. & Martinez N.D. (2005b) Body sizes of consumers and their resources. *Ecology*, 86, 2545

Brose U., Ostling A., Harrison K. & Martinez N.D. (2004) Unified spatial scaling of species and their trophic interactions. *Nature*, 428, 167-171

Brose U., Williams R.J. & Martinez N.D. (2003) Comment on "Foraging adaptation and the relationship between food-web complexity and stability". *Science*, 301, 918

Brose U., Williams R.J. & Martinez N.D. (2006) Allometric scaling enhances stability in complex food webs. *Ecology Letters*, 9, 1228-1236

Brown J.H., Gillooly J.F., Allen A.P., Savage V.M. & West G.B. (2004) Towards a metabolic theory of ecology. *Ecology*, 85, 1771-1789

Cattin M.F., Bersier L.F., Banašek-Richter C., Baltensperger R. & Gabriel J.P. (2004) Phylogenetic constraints and adaptation explain food-web structure. *Nature*, 427, 835-839

Cohen J.E. (1978) *Food webs and niche space*. Princeton University Press, NJ.

Cohen J.E. (1989) Version 1.0. Machine Readable Data Base of Food Webs: Ecologists Co-operative Web Bank (ECOWeb)

Cohen J.E. & Briand F. (1984) Trophic Links Of Community Food Webs. *Proceedings Of The National Academy Of Sciences Of The United States Of America-Biological Sciences*, 81, 4105-4109

Cohen J.E., Briand F. & Newman C.M. (1986) A Stochastic-Theory Of Community Food Webs.3. Predicted And Observed Lengths Of Food-Chains. *Proceedings Of The Royal Society Of London Series B-Biological Sciences*, 228, 317-353

Cohen J.E. & Newman C.M. (1985) A Stochastic-Theory Of Community Food Webs.1. Models And Aggregated Data. *Proceedings Of The Royal Society Of London Series B-Biological Sciences*, 224, 421-448

Darwin C. (1859) *The Origin of Species by means of natural selection*. John Murray, London.

De Angelis D.L. (1975) Stability and connectance in food web models. *Ecology*, 56, 238-243

De Angelis D.L., Goldstein R.A. & O'Neill R.V. (1975) A model for trophic interactions. *Ecology*, 56, 881-892

De Ruiter P., Neutel A.-M. & Moore J.C. (1995) Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science*, 269, 1257-1260

Dunne J.A. (2006) The network structure of food webs. In: *Ecological networks: linking structure to dynamics in food webs* (eds. Pascual M & Dunne JA), pp. 27-86. Oxford University Press

Dunne J.A., Williams R.J. & Martinez N.D. (2002) Food-web structure and network theory: The role of connectance and size. *Proceedings Of The National Academy Of Sciences Of The United States Of America*, 99, 12917-12922

Dunne J.A., Williams R.J. & Martinez N.D. (2004) Network structure and robustness of marine food webs. *Marine Ecology-Progress Series*, 273, 291-302

Elton C.S. (1933) *The ecology of animals*. Methuen, London.

Elton C.S. (1927) *Animal Ecology*. Sidgwick and Jackson, London.

Elton C.S. (1958) *Ecology of invasions by animals and plants*. Chapman & Hall, London.

Emmerson M. & Yearsley J.M. (2004) Weak interactions, omnivory and emergent food-web properties. *Proceedings Of The Royal Society Of London Series B-Biological Sciences*, 271, 397-405

Emmerson M.C. & Raffaelli D. (2004) Predator-prey body size, interaction strength and the stability of a real food web. *Journal of Animal Ecology*, 73, 399-409

Enquist B.J., West G.B., Charnov E.L. & Brown J.H. (1999) Allometric scaling of production and life-history variation in vascular plants. *Nature*, 401, 907-911

Erdös P. & Rényi A. (1960) On the Evolution of Random Graphs. *Publ. Math. Inst. Hung. Acad. Sci.*, 5, 17-61

Forbes S.A. (1887) The lake as a microcosm.

Fox L.R. (1975) Cannibalism in natural populations. *Annual review of Ecology and Systematics*, 6, 87-106

Fussmann G.F. & Heber G. (2002) Food web complexity and chaotic population dynamics. *Ecology Letters*, 5, 394-401

Gardner M.R. & Ashby W.R. (1970) Connectance of large dynamic (cybernetic) systems - critical values for stability. *Nature*, 228, 784

Gillooly J.F., Brown J.H., West G.B., Savage V.M. & Charnov E.L. (2001) Effects of size and temperature on metabolic rate. *Science*, 293, 2248-2251

Hairston N.G., Smith F.E. & Slobodkin L.B. (1960) Community structure, population control, and competition. *American Naturalist*, 94, 145-159

Hastings A. & Powell T. (1991) Chaos in a three-species food chain. *Ecology*, 72, 896-903

Havens K. (1992) Scale And Structure In Natural Food Webs. *Science*, 257, 1107-1109

Holling C.S. (1959a) The components of predation as revealed by a study of small-mammal predation of the European Pine Sawfly. *Canadian Entomologist*, 91, 293-320

Holling C.S. (1959b) Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, 7, 385-398

Hughes J.B., Daily G.C. & Ehrlich P.R. (1997) Population diversity: its extent and extinction. *Science*, 278, 689-692

Hunt H.W., Coleman D.C., Ingham E.R., Ingham R.E., Elliott E.T., Moore J.C., Rose S.L., Reid C.P.P. & Morley C.R. (1987) The Detrital Food Web In A Shortgrass Prairie. *Biology And Fertility Of Soils*, 3, 57-68

Hutchinson G.E. (1959) Homage to Santa Rosalia, or why are there so many kinds of animals? *American Naturalist*, 93, 145-159

Jeschke J.M., Kopp M. & Tollrian R. (2004) Consumer-food systems: why type I functional responses are exclusive to filter feeders. *Biological Reviews*, 79, 337-349

Jonsson T. & Ebenman B. (1998) Effects of predator-prey body size ratios on the stability of food chains. *Journal Of Theoretical Biology*, 193, 407-417

Kleiber M. (1932) Body size and metabolism. *Hilgardia*, 6, 315-332

Kleiber M. (1947) Body size and metabolic rate. *Physiological Reviews*, 27, 511-541

Kleiber M. (1961) *The Fire of Life: An Intruduction to Animal Energetics*. John Wiley & Sons.

Kondoh M. (2003) Foraging adaptation and the relationship between food-web complexity and stability. *Science*, 299, 1388-1391

Lawlor L.R. (1978) A comment on randomly constructed model ecosystems. *American Naturalist*, 112, 445-447

Lindstedt S.L. & Calder W.A.I. (1981) Body size, physiological time and longevity of homeothermic animals. *The Quarterly Review of Biology*, 56, 1-16

Lotka L. (1925) *Elements of physical biology*. Williams & Wilkins, Baltimore.

MacArthur R.H. (1955) Fluctuations of animal populations, and a measure of community stability. *Ecology*, 36, 533-536

MacArthur R.H. (1957) On the relative abundance of bird species. *Proceedings of the National Academy of Science of the United States of America*, 43, 293-295

MacArthur R.H. (1958) Population ecology of some warblers of northeastern coniferous forest. *Ecology*, 39, 599-619

Makarieva A.M., Gorshkova V.G. & Li B.L. (2005a) Energetics of the smallest: do bacteria breathe at the same rate as whales? *Proceedings Of The Royal Society B-Biological Sciences*, 272, 2219-2224

Makarieva A.M., Gorshkova V.G. & Li B.L. (2005b) Revising the distributive networks models of West, Brown and Enquist (1997) and Banavar, Maritan and Rinaldo (1999): Metabolic inequity of living tissues provides clues for the observed allometric scaling rules. *Journal of Theoretical Biology*, 237, 291-301

Martinez M.D. (1994) Scale-dependent constraints on food-web structure. *American Naturalist*, 144, 935-953

Martinez N.D. (1991) Artifacts Or Attributes -- Effects Of Resolution On The Little-Rock Lake Food Web. *Ecological Monographs*, 61, 367-392

Martinez N.D. (1992) Constant connectance in community food webs. *American Naturalist*, 139, 1208-1218

Martinez N.D. (1993) Effects of scale on food web structure. *Science*, 260, 242-243

Martinez N.D., Hawkins B.A., Dawah H.A. & Feifarek B.P. (1999) Effects of sampling effort on characterization of food-web structure. *Ecology*, 80, 1044-1055

Martinez N.D., Williams R.J. & Dunne J.A. (2006) Diversity, complexity, and persistence in large model ecosystems. In: *Ecological Networks: Linking Structure to Dynamics in Food Webs* (eds. Pascual M & Dunne JA), pp. 163-185. Oxford University Press, Oxford

May R.M. (1972) Will a large complex system be stable? *Nature*, 238, 413-414

May R.M. (1973) *Stability and complexity in model ecosystems*. Princeton University Press, Princeton, NJ.

McCann K. & Hastings A. (1997) Re-evaluating the omnivory-stability relationship in food webs. *Proceedings Of The Royal Society Of London Series B-Biological Sciences*, 264, 1249-1254

McCann K., Hastings A. & Huxel G.R. (1998) Weak trophic interactions and the balance of nature. *Nature*, 395, 794-798

McCann K. & Yodzis P. (1994) Biological conditions for chaos in a three-species food chain. *Ecology*, 75, 561-564

McCann K.S. (2000) The diversity-stability debate. *Nature*, 405, 228-233

Memmott J., Martinez N.D. & Cohen J.E. (2000) Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web. *Journal of Animal Ecology*, 69, 1-15

Merian M.S. (1679) *Der Raupen wunderbare Verwandlung und sonderbare Blumennahrung*. 3 Bände, Graff, Nürnberg 1679-1683

Merian M.S. (1705) *Metamorphosis insectorum Surinamensium*. Amsterdam 1705. Reprint, Leipzig 1975

Montoya J.M., Pimm S.L. & Sole R.V. (2006) Ecological networks and their fragility. *Nature*, 442, 259-264

Montoya J.M. & Solé R.V. (2003) Topological properties of food webs: from real data to community assembly models. *Oikos*, 102, 614-622

Neutel A.-M., Heesterbeek J.A.P. & De Ruiter P.C. (2002) Stability in real food webs: weak links in long loops. *Science*, 296, 1120-1123

Odum E. (1953) *Fundamentals of Ecology*. Saunders, Philadelphia.

Pierce W.D., Cushman R.A. & Hood C.E. (1912) The insect enemies of the cotton boll weevil. *USDA Bur. Entomol. Bull.*, 100, 9-99

Pimm S.L. (1979) Complexity And Stability - Another Look At Macarthur Original Hypothesis. *Oikos*, 33, 351-357

Pimm S.L. & Lawton J.H. (1977) Number Of Trophic Levels In Ecological Communities. *Nature*, 268, 329-331

Pimm S.L., Russell G.J., Gittleman J.L. & Brooks T.M. (1995) The Future of Biodiversity. *Science*, 269, 347-350

Polis G.A. (1991) Complex trophic interactions in deserts: an empirical critique of food-web theory. *American Naturalist*, 138, 123-155

Polis G.A. (1998) Stability is woven by complex webs. *Nature*, 395, 744-745

Post D.M., Conners M.E. & Goldberg D.S. (2000a) Prey preference by a top predator and the stability of linked food chains. *Ecology*, 81, 8-14

Post D.M., Pace M.L. & Hairston N.G., Jr. (2000b) Ecosystem size determines food-chain length in lakes. *Nature*, 405, 1047-1049

Rall B.C., Guill C. & Brose U. (2008) Food-web connectance and predator interference dampen the paradox of enrichment. *Oikos*, doi: 10.1111/j.2007.0030-1299.15491.x

Reuman D.C. & Cohen J.E. (2005) Estimating relative energy fluxes using the food web, species abundance, and body size. In: *Advances in Ecological Research, Vol 36*, pp. 137-182

Rosenzweig M.L. & MacArthur R.H. (1963) Graphical representation and stability conditions of predator-prey interactions. *American Naturalist*, 97, 209-223

Rubner M. (1883) Über den Einfluß der Körpergröße auf den Stoff- und Kraftwechsel. *Zeitschrift für Biologie*, 19, 535-562

Salà O.E., Chapin F.S., III, Armesto J.J., Berlow E., Bloomfield J., Dirzo R., Huber-Sanwald E., Huenneke L.F., Jackson R.B., Kinzig A., Leemans R., Lodge D.M., Mooney H.A., Oesterheld M., Poff N.L., Sykes M.T., Walker B.H., Walker M. & Wall D.H. (2000) Global biodiversity scenarios for the year 2100. *Science*, 287, 1771-1774

Savage V.M., Gillooly J.F., Brown J.H., West G.B. & Charnov E.L. (2004a) Effects of body size and temperature on population growth. *American Naturalist*, 163, E429-E441

Savage V.M., Gillooly J.F., Woodruff W.H., West G.B., Allen A.P., Enquist B.J. & Brown J.H. (2004b) The predominance of quarter-power scaling in biology. *Functional Ecology*, 18, 257-282

Shelford V.E. (1913) *Animal Communities in temperate America as illustrated in the Chicago Region: A study in animal Ecology*. University of Chicago Press, Chicago, IL.

Sheppard S.K., Bell J., Sunderland K.D., Fenlon J., Skervin D. & Symondson W.O.C. (2005) Detection of secondary predation by PCR analyses of the gut contents of invertebrate generalist predators. *Molecular Ecology*, 14, 4461-4468

Stouffer D.B., Camacho J. & Amaral L.A.N. (2006) A robust measure of food web intervality. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 19015-19020

Stouffer D.B., Camacho J., Guimera R., Ng C.A. & Amaral L.A.N. (2005) Quantitative patterns in the structure of model and empirical food webs. *Ecology*, 86, 1301-1311

Summerhayes V.S. & Elton C.S. (1923) Contributions to the Ecology of Spitzbergen and Bear Island. *J. Ecol.*, 214-286

Summerhayes V.S. & Elton C.S. (1928) Further Contributions to the Ecology of Spitzbergen and Bear Island. *J. Ecol.*, 193-268

Sutherland J.W. (1989) Andriondack Biota Project. In: *DEC publication*, p. 720. Lake Services Section, New York State Department of Environmental Conservation, New York

van der Meer J. (2006) Metabolic theories in ecology. *Trends in Ecology & Evolution*, 21, 136-140

Vandermeer J. (2006) Omnivory and the stability of food webs. *Journal Of Theoretical Biology*, 238, 497-504

Volterra V. (1926) Fluctuations in the abundance of a species considered mathematically. *Nature*, 118, 558-560

Warren P.H. (1989) Spatial and Temporal Variation in the Structure of a Fresh-Water Food Web. *Oikos*, 55, 299-311

Warren P.H. & Lawton J.H. (1987) Invertebrate Predator-Prey Body Size Relationships - an Explanation for Upper-Triangular Food Webs and Patterns in Food Web Structure. *Oecologia*, 74, 231-235

Weitz J.S. & Levin S.A. (2006) Size and scaling of predator-prey dynamics. *Ecology Letters*, 9, 548-557

West G.B., Brown J.H. & Enquist B.J. (1997) A general model for the origin of allometric scaling laws in biology. *Science*, 276, 122-126

West G.B., Brown J.H. & Enquist B.J. (1999) The fourth dimension of life: fractal geometry and allometric scaling of organisms. *Science*, 284, 1677-1680

Williams R.J. & Martinez N.D. (2000) Simple rules yield complex food webs. *Nature*, 404, 180-183

Williams R.J. & Martinez N.D. (2004a) Limits to trophic levels and omnivory in complex food webs: Theory and data. *American Naturalist*, 163, 458-468

Williams R.J. & Martinez N.D. (2004b) Stabilization of chaotic and non-permanent food web dynamics. *European Physical Journal B*, 38, 297-303

Williams R.J., Martinez N.D., Berlow E.L., Dunne J.A. & Barabási A.-L. (2002) Two degrees of separation in complex food webs. *Proceedings of the National Academy of Science*, 99, 12913-12916

Winemiller K.O. (1989) Must connectance decrease with species richness? *American Naturalist*, 134, 960-968

Winemiller K.O. (1990) Spatial And Temporal Variation In Tropical Fish Trophic Networks. *Ecological Monographs*, 60, 331-367

Woodward G. & Hildrew A.G. (2001) Invasion of a stream food web by a new top predator. *Journal of Animal Ecology*, 70, 273-288

Yodzis P. (1981) The Stability of Real Ecosystems. *Nature*, 289, 674-676

Yodzis P. & Innes S. (1992) Body size and consumer-resource dynamics. *American Naturalist*, 139, 1151-1175

Chapter 2

The diversity and identity of predators drive interaction strengths and trophic cascades in a montane food web

Food chain. The herbivore willow leaf beetle (*Chrysomela aeneicollis*) feeds on the willow *Salix orestera* at high elevations in California. The picture shows one third instar larvae of the beetle (left, black with white dots) and one pupa (right). Feeding damage on the willow is visible on the right edge of the leaf. Larvae of the hover fly *Parasyrphus melanderi* (center, pale with white spots) feed exclusively on these beetles at montane field sites.

Photo: Sonja B. Otto

2.1 Abstract

Declining predator diversity may drastically affect the biomass and productivity of herbivores and plants. Understanding how changes in predator diversity can propagate through food webs to alter ecosystem function is one of the most challenging ecological research topics today. We studied the effects of predator removal in a simple natural food web in the Sierra Nevada mountains of California (USA). By excluding the predators of the third trophic level of a food web in a full-factorial design, we monitored cascading effects of varying predator diversity and composition on the herbivorous beetle *Chrysomela aeneicollis* and the willow *Salix orestera*, which compose the first and second trophic levels of the food web. Decreasing predator diversity increased herbivore biomass and survivorship, and consequently increased the amount of plant biomass consumed via a trophic cascade. Despite this simple linear mean effect of diversity on the strength of the trophic cascade, we found additivity, compensation, and interference in the effects of multiple predators on herbivores and plants. Herbivore survivorship and predator–prey interaction strengths varied with predator diversity, predator identity, and the identity of coexisting predators. Additive effects of predators on herbivores and plants may have been driven by temporal niche separation, whereas compensatory effects and interference occurred among predators with a similar phenology. Together, these results suggest that while the general trends of diversity effects may appear linear and additive, other information about species identity was required to predict the effects of removing individual predators. In a community that is not temporally well-mixed, predator traits such as phenology may help predict impacts of species loss on other species. Information about predator natural history and food web structure may help explain variation in predator diversity effects on trophic cascades and ecosystem function.

2.2 Introduction

A key challenge of environmental biology is to understand how biodiversity loss influences ecosystem function (reviewed by Hooper *et al.* 2005). Most early seminal studies of the relationship between biodiversity and ecosystem function focused on plant diversity and plant productivity (Tilman 1996, 1997; Hooper and Vitousek 1997). However, some studies suggest that high trophic level species such as top predators may be more vulnerable to extinction than species at lower trophic levels (e.g., Pimm *et al.* 1988, Petchey *et al.* 1999). Initial theoretical and empirical studies suggest that the relationship between diversity and ecosystem function is more complex and variable at higher trophic levels (Thébault and Loreau 2003, Worm and Duffy 2003,

Petchey *et al.* 2004, Hooper *et al.* 2005). Thus, it is critical to understand how biodiversity loss at higher trophic levels may propagate through a web of species interactions to influence ecosystem function (Bascompte *et al.* 2005, Myers *et al.* 2007). One promising approach for addressing this challenge is to integrate subdisciplines of studies that focus on effects of diversity, per se, on ecosystem function with those that focus on predator–prey dynamics and interaction strengths (Ives *et al.* 2005, Wootton and Emmerson 2005). We focus here on three mechanisms proposed by Ives (2005) which regulate how predator diversity can influence both ecosystem function and predator–prey interaction strengths. First, the "sampling effect" or "selection-probability effect" occurs when one species of a predator guild dominates effects of that guild on the prey. Thus, effects of predator diversity on prey biomass may be driven primarily by whether one strong (or "keystone") predator is present (e.g., Navarrete and Menge 1996). In this case, predator identity drives the effect of predator diversity on prey biomass and potential cascading effects on plant biomass production. Second, additive effects of different predators on a prey species are likely when exploitative competition among predators is weak, because each of them occupies a different niche (Chang 1996, Snyder and Ives 2003) or targets different life history stages of the prey. This is similar to the notion of "complementarity" among plants in resource use, which would cause a monotonic increase in productivity with increased plant diversity (e.g., Tilman *et al.* 1996). If additive effects of individual predators are of similar strength, effects of predators on shared prey and cascading effects on plant biomass production should depend on the number of predators, but be independent of their identity. Third, multiple predators can have "redundant" or "compensatory" effects on their prey if removal of one is compensated by increases in prey consumption by others (Navarrete and Menge 1996). This is similar to the "insurance hypothesis" (e.g., Tilman 1996, Yachi and Loreau 1999), where functional "redundancy" among species with high niche overlap increases stability of ecosystem function (Walker 1992, Naeem and Li 1997, Tilman 1999). Compensatory effects of predators would suggest that effects of predator removal on prey biomass and plant production should be small until the last predator is removed, irrespective of its identity. Most experimental studies of predator diversity effects on ecosystem function in complex food webs have been restricted to microcosms (Naeem and Li 1997, 1998, Gamfeldt *et al.* 2005) or "food web compartments" which were studied in mesocosm enclosures (Petchey and Gaston 2002, Schmitz and Sokol-Hessner 2002, Cardinale *et al.* 2003, Finke and Denno 2004, 2005, Snyder *et al.* 2006, Straub and Snyder 2006). Most of these studies also do not incorporate a full factorial manipulation of all predators (but see Schmitz and Sokol-Hessner 2002 for an exception) and thus do not quantify non-additive interactions

among all natural predators. Similarly, these enclosure studies cannot examine interactions among predators with different phenologies. Here, we carry out a full-factorial removal of all predators at the third trophic level in a simple terrestrial food web in the Sierra Nevada mountains of California (USA). This is, to our knowledge, the first full-factorial removal experiment of an entire trophic level under natural field conditions. We quantified prey survival over time and explored how predator–herbivore interaction strengths and potentially non-additive predator effects govern how consumer diversity influences both herbivore and plant biomass. Finally, by examining individual effects of each predator on beetle survivorship and biomass, we distinguish between effects of (1) consumer identity (i.e., sampling effect), (2) consumer additivity, and (3) consumer compensation.

2.3 Methods

Field site and food web. The experimental units were located at the South Fork of Bishop Creek (2860 m) in the Sierra Nevada range in eastern California (37°18' N, 118°56' W). Experiments were conducted from June 23rd 2005, shortly after snow melt, to August 10th 2005. Manipulations were carried out on the willow *Salix orestera* C. K. Schneid, which occurs along creeks and in bogs from 2800–3500 m altitude (Smiley and Rank 1991). We quantified separate and interactive effects of the three main predator groups (Smiley and Rank 1986) that were most abundant and fed frequently on larvae of the willow leaf beetle *Chrysomela aeneicollis* Schaeffer (Coleoptera: Chrysomelidae). We quantified their effects on beetle survivorship and biomass, as well as on the amount of willow leaf tissue consumed by the beetles. The beetles lay egg clutches on the lower surface of willow leaves. After hatching, *Chrysomela* larvae feed on *Salix* leaf tissue for three instars and then migrate to the tips of willow shoots to pupate (see Photos 2.1 a-e for live stages).

Photo 2.1 | Life history of *Chrysomela aeneicollis*. (a) Egg clutch, **(b)** first instar larvae, **(c)** third instar larvae, **(d)** pupa and **(e)** adult beetle. Photos: S.B. Otto.

In the experimental area, predators on these beetles include crawling predators such as a predatory red mite (Prostigmata: Holotrombidae), ants belonging to the genera *Formica* and *Camponotus*, a syrphid fly *Parasyrphus melanderi* Curran (Diptera: Syrphidae), and a solitary wasp *Symmorphus cristatus* Saussure (Vespidae: Eumenidae) (see Photos 2.2a-d). As it was impossible to exclude crawling predators individually, and as they consume the same instar stages of the beetles, we aggregated them as a functional predator-type and will subsequently refer to them as crawlers.

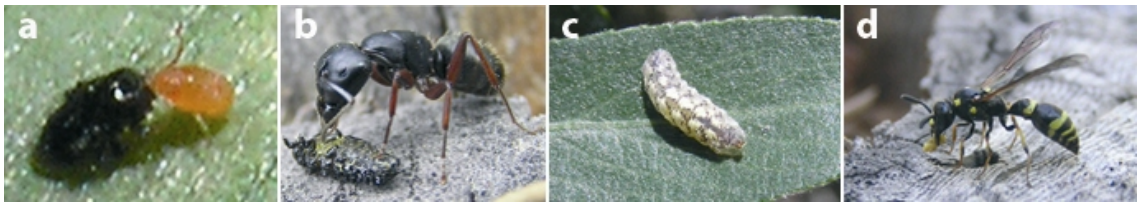


Photo 2.2 | The main predators of *Chrysomela aeneicollis*. (a) Predatory red mite, sucking on a first instar larvae of the beetles, **(b)** the ant *Camponotus spec.*, **(c)** maggot of the hover fly *Parasyrphus melanderi*, and **(d)** the solitary wasp *Symmorphus cristatus.* Photos: S.B. Otto.

Syrphid flies and wasps are specialized predators that consume exclusively *C. aeneicollis* larvae. The crawlers, syrphid flies, and wasps have different phenologies and feeding niches: they occur during different time periods, and they feed on different larval stages. The crawlers prey on eggs and first instar larvae of the beetles. Female syrphid flies lay one to nine eggs on young beetle egg clutches (three small white syrphid eggs are visible on Photo 2.1a). Between hatching and pupation, syrphid larvae feed on eggs and first to third instar beetle larvae (Rank and Smiley 1994)(see cover picture). The wasps appear later in the season and prey only on third instar beetle larvae (Sears *et al.* 2001).

Experimental treatments and response variables. On June 23rd 2005, we applied three different exclusion methods in a full-factorial design to branches that each contained one beetle egg clutch. While there was some natural variation in the number of eggs per clutch (clutch size = 43.1 ± 4.8 eggs; mean ± SD), there was no significant difference among treatments in initial egg number (ANOVA, $F_{21,50} = 1.27$, $p = 0.24$). In each treatment, one or more predators were excluded, which yielded eight treatments with all combinations of crawlers, syrphid flies, and wasps excluded vs. not excluded. We used one individual branch with one beetle egg clutch per willow clone as an experimental unit (replicate) to maximize replication across host plant individuals. With nine replicates per treatment, a total of 72 experimental units on 72 different willow clones were under observation. We isolated manipulated branches

from neighbouring branches by clipping surrounding foliage to avoid the migration of beetle larvae or crawling predators. Only newly laid beetle egg clutches (discernable by colour and smooth surface) were included in experimental branches, which minimized variation in the time exposed to predators. Crawling predators were excluded by Tanglefoot (Tanglefoot^{TM}, Grand Rapids, Michigan, USA), a sticky preparation of castor oil and natural gum resins that was applied at the base of observed branches and thus prevented access of mites and ants. Flying predators were excluded by enclosing branches in mesh bags that allowed access by crawling predators. To exclude syrphid flies, we prevented females from ovipositing on beetle egg clutches by enclosing branches in a mesh bag until beetle larvae reached the second instar. These bags were removed in treatments where wasps were not to be excluded before larvae reached the third instar, which was when they were vulnerable to wasp predation. To exclude the wasps, branches were enclosed in mesh bags before beetle larvae reached the third instar. All treatments were applied under natural conditions without affecting densities of the other predator species, beetle densities, or the proportions of different beetle larval stages in the treatments.

We monitored total beetle abundance regularly from June 24th to August 9th 2005. At each monitoring day, we calculated beetle survivorship as the percentage of surviving beetle individuals relative to the initial number of eggs of each clutch. At the end of the experiment, we collected all surviving beetle individuals and measured their total biomass for each replicate. In treatments without mesh bags, some beetle adults left the branches before being collected, which resulted in a number of pupal skins that exceeded the number of adult beetles. In these few cases, we multiplied the number of excess pupal skins by the averaged beetle mass of hatched individuals (19.4 ± 3.7 mg, mean ± SD, n = 76 new adults) and added this value to the beetle biomass on this branch. This introduced a small error by overestimating total beetle biomass in treatments with smaller than average larvae and underestimating total beetle biomass in treatments with larger than average larvae. To evaluate whether this error affected the results, all analyses were carried out with both beetle biomass and proportional survivorship as response variables. We calculated the average survivorship of herbivores during the experiment by an average survivorship index (Breden and Wade 1985, Rank 1994). It ranges from zero to one and measures the area beneath the survival curve of all individuals through the time of the whole experiment, divided by the total area if all initial larvae had survived to the last count (Breden and Wade 1987, Rank 1994). In contrast to final beetle number, this variable accounts for beetle survival during the entire time course of the experiment. In particular, it avoids problems with parametric statistical analyses (heteroscedasticity) that emerge when a high proportion of zeros are present in the data. For instance, in 32 of our replicates,

all beetles were consumed by the end of the experiment and the final beetle biomass equaled zero. To quantify the biomass of plant tissue eaten, we collected all leaves of the replicates which showed signs of consumption on August 9th. We used a grid-count method (0.5 cm² cell size) to estimate the foliage area eaten, *f*. We weighted the leaf samples with leaf area, *T*, measured their biomass, B_T, and calculated the biomass of leaf tissue eaten (in grams), B_t by $B_t = (B_T / T) / f$.

Statistical analyses and interaction strengths. To distinguish differences in effects of each predator and combination of predators on beetle survival in time we used repeated-measures ANOVA, with each predator combination as a grouping factor (or interaction among grouping factors) and proportion survival as the dependent variable. To evaluate the significance of predator effects at the end of our experiments, we used $\log_{10}$-transformed beetle biomass, $\log_{10}$-transformed plant biomass eaten, and average survivorship of the beetles as dependent variables. With standard least squares three-way full-factorial ANOVAs we tested for effects of predator removal treatments on beetle biomass and survivorship (percentage of initial egg number) at the end of the experiment. In linear least-square regressions, we determined the impact of predator diversity on the dependent variables. Additionally, we carried out ANCOVAs with $\log_{10}$beetle biomass or average beetle survivorship as dependent variable, predator diversity as a continuous predictor, and the presence or absence of the three predators as categorical independent variables. Significant effects of the predator presence–absence variables indicate predator identity effects.

To disentangle the effects of predator diversity from those of changes in total predator density, we compared our measured response variables ($\log_{10}$beetle biomass, $\log_{10}$plant biomass eaten, and average survivorship of the beetles) for predator diversity levels of two and three to expected values based on extrapolations of the effects of each predator group alone. The expected effects of multiple predators, $\sigma_{(i+j)}$, were calculated as $\sigma_{(i+j)} = \sigma_i * \sigma_j / \sigma_{NP}$, where σ_i is the proportion of the effect of one predator on each response variable, σ_j is the proportion of the effect of a second predator, and σ_{NP} is the value of the response variable when no predators are present (Vonesh and Osenberg 2003). An expected value within the standard error of the empirically measured effects indicates additivity, whereas an expected value outside the standard error indicates non-additivity of multiple predators.

The Interaction Strength (IS) between a predator and the beetles was calculated as the $\log_{10}$ ratio between beetle biomass, *B*, in the presence and absence of the predator: $IS_{pred/prey} = \log_{10}(B^{+pred} / B^{-pred})$. We distinguished interaction strengths between any predator and the beetles, depending on predator diversity level and the identity of coexisting predators. In a community of three predator species (e.g., i, j, k),

the interaction strengths between, for example, predator i and the beetles can be measured unambiguously at predator diversity levels of one (predator i present, $B^{+i,-j,-k}$ vs. no predator present, $B^{-i,-j,-k}$) and three (all three predators present, $B^{+i,+j,+k}$, vs. only the two other predators present, $B^{-i,+j,+k}$). At a predator diversity level of two, however, two different interaction strengths describe the effects of predator i on the beetles depending on whether it coexists with predator j (predators i and j present, $B^{+i,+j,-k}$, vs. only predator j present, $B^{-i,+j,-k}$) or whether it coexists with predator k (predators i and k present, $B^{+i,-j,+k}$, vs. only predator k present, $B^{-i,-j,+k}$). These calculations allow analyses of variation in pairwise interaction strengths depending on the identity of coexisting predators. The means and standard errors of interaction strengths at predator diversity levels of one and three were calculated by bootstrapping (2000 random samples of the original data set). We used an ANOVA to test for significant differences among the interaction strengths. The additivity hypothesis predicts that the interaction strength of a predator is independent of the number and identity of the coexisting predators and thus should be similar for the treatments. The redundancy hypothesis predicts that the interaction strength of a predator at the diversity level of one should be substantially higher than its interaction strengths at higher diversity levels, due to compensatory effects of other predators. A positive interaction strength of predator i when coexisting with predator j indicates interference between predators i and j, resulting in a higher prey biomass when both predators coexist, compared to treatments without i.

2.4 Results

Beetle survival over time in treatments with total predator exclusion (Figure 2.1, solid line) was significantly higher than in control treatments without predator removal (natural conditions, Figure 2.1, dashed line; repeated-measures ANOVA, $F_{1,16} = 22.38$, $p = 0.0002$). A significant mortality effect of predators on beetles, i.e., the difference between the bold and dashed lines in Figure 2.1, was observed early in the season (day 7, repeated measures ANOVA, $p = 0.044$) and increased during the experiment. At the end of the experiment, the survivorship of the beetles in the treatment without any predators was 36.9 ± 10.2% (mean ± SE), but survivorship was 1.1 ± 0.9% on control branches that were exposed to all predators (Figure 2.1). Overall, ANOVAs showed significant effects of the predator removal treatments on $\log_{10}$-transformed beetle biomass ($F_{7,63} = 2.75$, $p = 0.015$) and beetle survivorship ($F_{7,63} = 3.53$, $p = 0.003$). In both ANOVAs, we found significant interaction terms between crawlers and syrphid flies (for $\log_{10}$-transformed beetle biomass, $p = 0.033$; for beetle survivorship, $p = 0.01$) and a significant main effect of the wasps (for $\log_{10}$-transformed beetle

biomass, p = 0.046; for beetle survivorship, p = 0.015), whereas all other two-way and three-way interaction terms were not significant.

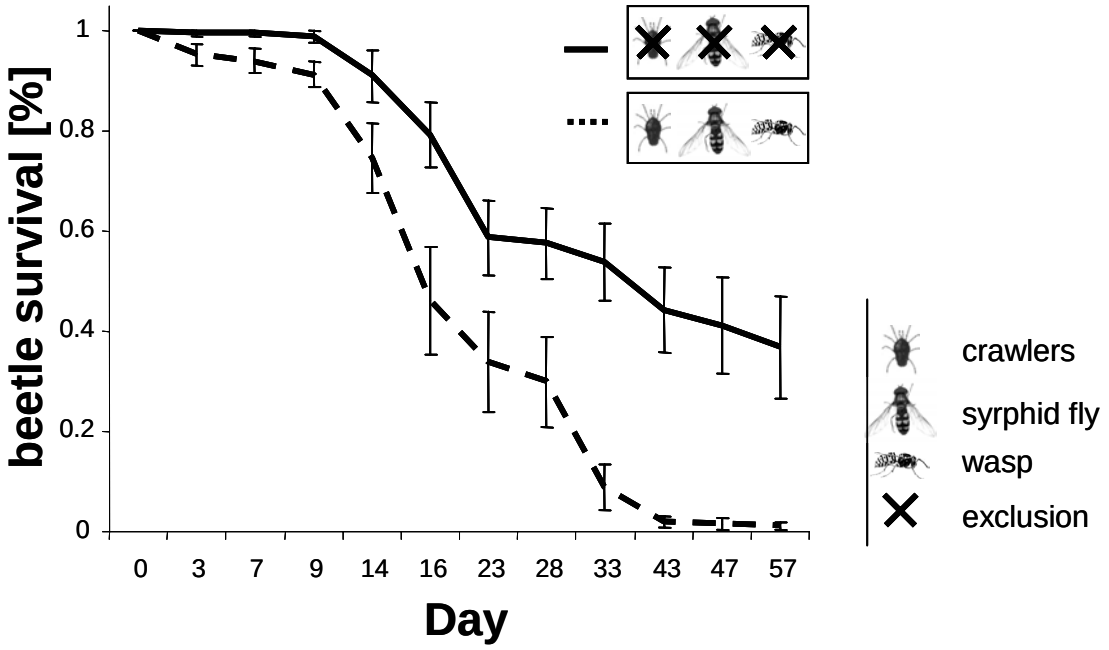


Figure 2.1 | Time course of willow leaf beetle (*Chrysomela aeneicollis*) survival (percentage of initial egg number, mean ± SE) from day 0 (experimental set up) to day 57 (sampling and counting of hatched beetle adults): comparison of treatments with all three predators (dashed line) and with total predator exclusion (solid line). The x-axis depicts data on sampling dates rather than over a continuous time course. Curves differ significantly (repeated-measures ANOVA: $F_{1,16} = 22.38$, p = 0.0002).

In treatments with single predators (predator diversity level of one), beetle survival was lower (Figure 2.2a–c, dashed lines) than under total predator exclusion (Figure 2.2a–c, solid lines). The grey bars parallel to the x-axis in Figure 2.2a–c indicate the approximate time periods of the presence of the different predators in the food web (hereafter, phenology) over the course of our study. Thus, the crawlers (Figure 2.2a) appear earlier in the season than the syrphid flies (Figure 2.2b), but then the presence of both predators overlaps considerably, whereas the wasps enter the system later and overlap only for approximately two weeks with the syrphid flies (Figure 2.2c). Each predator had a stronger effect when it was the only predator in the food web (Figure 2.2a–c) than when it was removed from an intact community with all predators present (Figure 2.2d–f). When individual predator treatments were compared to total predator

exclusions, crawlers and syrphid flies significantly reduced beetle larvae survival over time (Figure 2.2a, b; see legend for RM [repeated-measures] ANOVA results). The wasps also reduced the survival of the beetle larvae, but this effect was not statistically significant (Figure 2.2c; see legend for RM-ANOVA results). When individual predator removals were compared to un-manipulated treatments (i.e., all predators present), none of the predators had significant effects on beetle survival over the time course of the experiment (Figure 2.2d–f, see legend for RM-ANOVA results). However, in contrast to the other two predators, the effects of wasp removal were marginally significant on the last three sampling dates (Figure 2.2f, see legend for last day). In general, the trends in Figure 2.2 suggest ecologically significant predator effects on beetle survivorship that are consistent with the predator's appearance in the food web: When each predator is considered in isolation (Figure 2.2a–c), the effect of crawlers on beetle survival magnified after day 9 (late egg stage and some first instar larvae, Figure 2.2a), the effect of syrphid flies on beetles became distinct after day 23 (most syrphid maggots hatched at the time of late first instar and early second instar beetle larvae; Figure 2.2b), and the trend for wasp effects on beetles is largest after day 28 (late second and early third-instar larvae, Figure 2.2c).

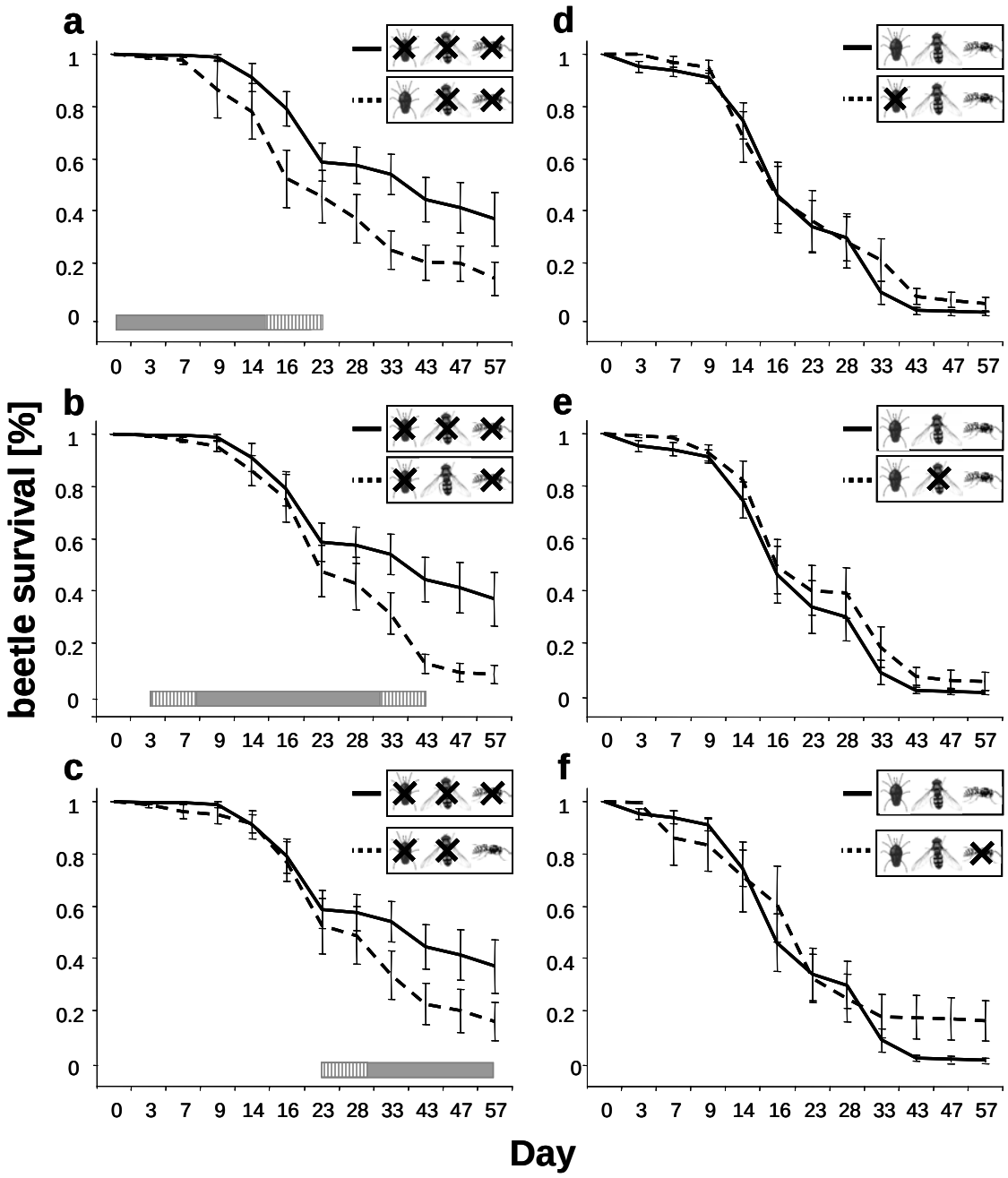


Figure 2.2 | Time course of beetle survival (percentage of initial egg number, mean ± SE) from day 0 (experimental set up) to day 57 (sampling and counting of hatched beetle adults): The left-hand column shows the comparison of total predator exclusion (solid lines) vs. single-predator presence (dashed lines) of **(a)** "crawlers", **(b)** syrphid flies, or **(c)** wasps (see Figure 2.1 for symbol explanation). The right-hand column shows comparison of the control treatment (no predator removed, solid lines) vs. single-predator exclusion (dashed lines) of **(d)** "crawlers", **(e)** syrphid flies, or **(f)** wasps. Curves in (a) and (b) differ significantly, curves in (c)–(f) do not, (repeated-measures ANOVA, (a) $F_{1,16} = 5.28$, $p = 0.04$; (b) $F_{1,16} = 6.90$, $p = 0.02$; (c) $F_{1,16} = 2.25$, $p = 0.15$; (d) $F_{1,16} = 0.21$, $p = 0.65$; (e) $F_{1,16} = 1.12$, $p = 0.31$; (f) $F_{1,16} = 0.31$, $p = 0.59$; ANOVA on day 57, (a) $p = 0.077$, (b) $p = 0.017$, (c) $p = 0.114$, (d) $p = 0.152$, (e) $p = 0.269$, (f) $p = 0.067$). The x-axis depicts data on sampling dates rather than over a continuous time course. The grey horizontal bars indicate the phenology of the predators in the food web; dashed ends indicate that phenology is not bound to strict dates.

Increasing predator diversity caused a significant decrease in (1) $\log_{10}$-transformed beetle biomass (Figure 2.3a), (2) $\log_{10}$-transformed plant biomass consumed (Figure 2.3b), and (3) average survivorship of the beetles (Figure 2.3c). While these central tendencies were highly significant ($P < 0.002$ in all cases), the variance within treatments was substantial ($R^2 < 0.22$). A three-species predator community reduced the biomass of the beetles by 96.15% compared to the all-predator exclusion treatments. Increasing predator diversity also increased the strength of a trophic cascade through the food web to significantly decrease the amount of plant biomass consumed (Figure 2.3b). The complete predator community reduced the amount of plant biomass consumed by 75% compared to replicates where all predators were removed from the food web. Increasing predator diversity from zero to three reduced the absolute amount of plant biomass consumed (3.75 g) 15 times more than it reduced beetle biomass (0.25 g). The effects of individual predators on the amount of plant biomass removed (Figure 2.3b) were similar to those on beetle biomass (Figure 2.3a). The exception to this pattern was that crawlers, as single predators at a predator diversity level of one, reduced beetle biomass more than the wasps (Figure 2.3a), whereas the wasps reduced the amount of plant biomass consumed more strongly than the crawlers (Figure 2.3b). To evaluate whether the observed effect of increased predator diversity (Figure 2.3a–c) could be explained by increased predator density alone, we compared the observed effect to that expected based on extrapolations of the individual predator effects. Expected beetle biomasses at predator diversities of two and three lay within one standard error of the mean observed values, except for the treatment where syrphid flies and crawlers coexisted ($\log_{10}$-transformed beetle biomass mean [± SE], expected = 0.014, observed = 0.052 [±0.02]). The slope of the regression through the expected values (-0.028 ± 0.005 SE) is within one standard error of the regression slope through the observed values (regression details in legend to Figure 2.3a). The expected values for plant biomass eaten and the slope of the regression (slope = -0.16) are within one standard error of the observed values.

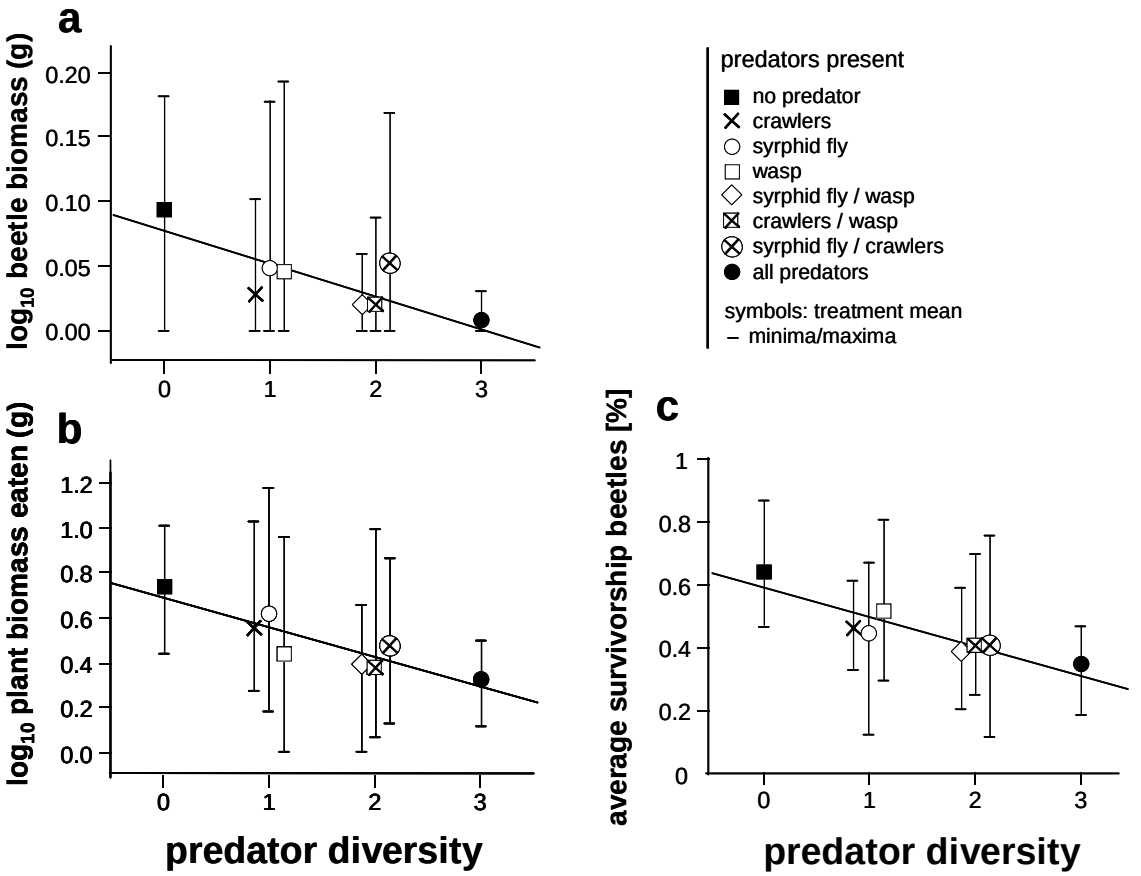


Figure 2.3 | Predator diversity effects on (a) $\log_{10}$-transformed beetle biomass (originally measured in grams), **(b)** the amount of $\log_{10}$-transformed plant biomass consumed by the beetles (originally measured in grams) and **(c)** the average survivorship of beetle individuals at the end of the experiment. Data columns are offset (at predator diversity levels of 1 and 2) by 0.02 cm for better determination of predator identity effects. Symbols show treatment means; whiskers indicate the treatment minima and maxima. Regression details follow (± SE): (a) $y = 0.077\ (\pm 0.01) - 0.025(\pm 0.007)x$, $R^2 = 0.16$, $F_{1,69} = 13.35$, $p = 0.0005$; (b) $y = 0.69\ (\pm 0.07) - 0.13\ (\pm 0.04)x$, $R^2 = 0.15$, $F_{2,57} = 10.66$, $p = 0.0018$; (c) $y = 0.59\ (\pm 0.03) - 0.09\ (\pm 0.02)x$, $R^2 = 0.22$, $F_{2,67} = 19.40$, $p < 0.0001$.

The expected values for the average survivorship of the beetles are all within the standard errors of the observed values except for a higher than expected survival in the treatment where all predators are present (expected = 0.29, observed [±SE] = 0.35 [±0.03]). The slope of the relationship between expected survivorship and predator diversity was marginally steeper than the observed slope (slope expected: -0.11, slope observed [±SE]: -0.09 [±0.02]).

To disentangle the effects of predator diversity and predator identity, we used an analysis of covariance with average beetle survivorship and $\log_{10}$ beetle biomass at the end of the experiments as response variables. These analyses suggest that the

predator effects we observed were driven by predator diversity but not the identity of present predators (beetle biomass, $p = 0.002$ and 0.33 for predator diversity and predator identity, respectively; average survivorship, $p = 0.0004$ and 0.56 for predator diversity and predator identity, respectively). Similar results were obtained with a type-I ANOVA, in which predator diversity was entered before predator identity.

Predator–prey interaction strengths (IS) varied with predator diversity (Figure 2.4a) and with the identity of coexisting predators (Figure 2.4b). The subsequent results describe trends in biomass-based interaction strengths, but qualitatively identical trends characterize interaction strengths analyses based on beetle survivorship at the end of the experiment. All predators had a strong effect on beetle biomass when no other predators co-occurred (predator diversity level equals one, Figure 2.4a) and the effect of crawlers was significantly stronger than the effects of syrphid flies or wasps (Tukey's HSD test, $p < 0.05$). When all three predators were present, however, wasp removal had a significantly stronger impact on beetle biomass than the removal of either crawlers or syrphid flies alone (Tukey's HSD test, $p < 0.05$; Figure 2.4a). The effect of the wasps on beetle biomass was similar at the predator diversity levels of one (i.e., single-predator community) and three (i.e., an "intact" community with all three predators; Figure 2.4a). In contrast, the crawlers and syrphid flies had significantly stronger effects on the beetles in the single-predator treatments than in the "intact" community of three predators (Tukey's HSD test, $p < 0.05$; Figure 2.4a). When predators were removed from a whole-predator community, the magnitude of their effects on beetles depended on the identity of the coexisting predator (Figure 2.4b). If the wasps coexisted with crawlers or syrphid flies, all effects on beetles were negative. However, if crawlers and syrphid flies coexisted in the food web, beetle biomass was on average higher in the presence of both predators than in treatments in which one of the predators had been removed (Figure 2.4b), indicating predator interference. Average body mass of beetle individuals (y) decreased significantly with increasing beetle abundance (A) at the end of the experiments (ordinary linear least square regression [LSR (± SE)]: $y = 0.022 (\pm 0.0008) - 0.0002 (\pm 0.00006)A$; $R^2 = 0.22$, $p = 0.003$), increasing beetle biomass (B; LSR(± SE): $y = 0.021 (\pm 0.0008) - 0.008 (\pm 0.004)B$; $R^2 = 0.13$, $p = 0.025$), and thus with decreasing predator diversity (D; LSR (± SE): $y = 0.017 (\pm 0.0009) - 0.002 (\pm 0.0006)D$; $R^2 = 0.19$, $p = 0.006$).

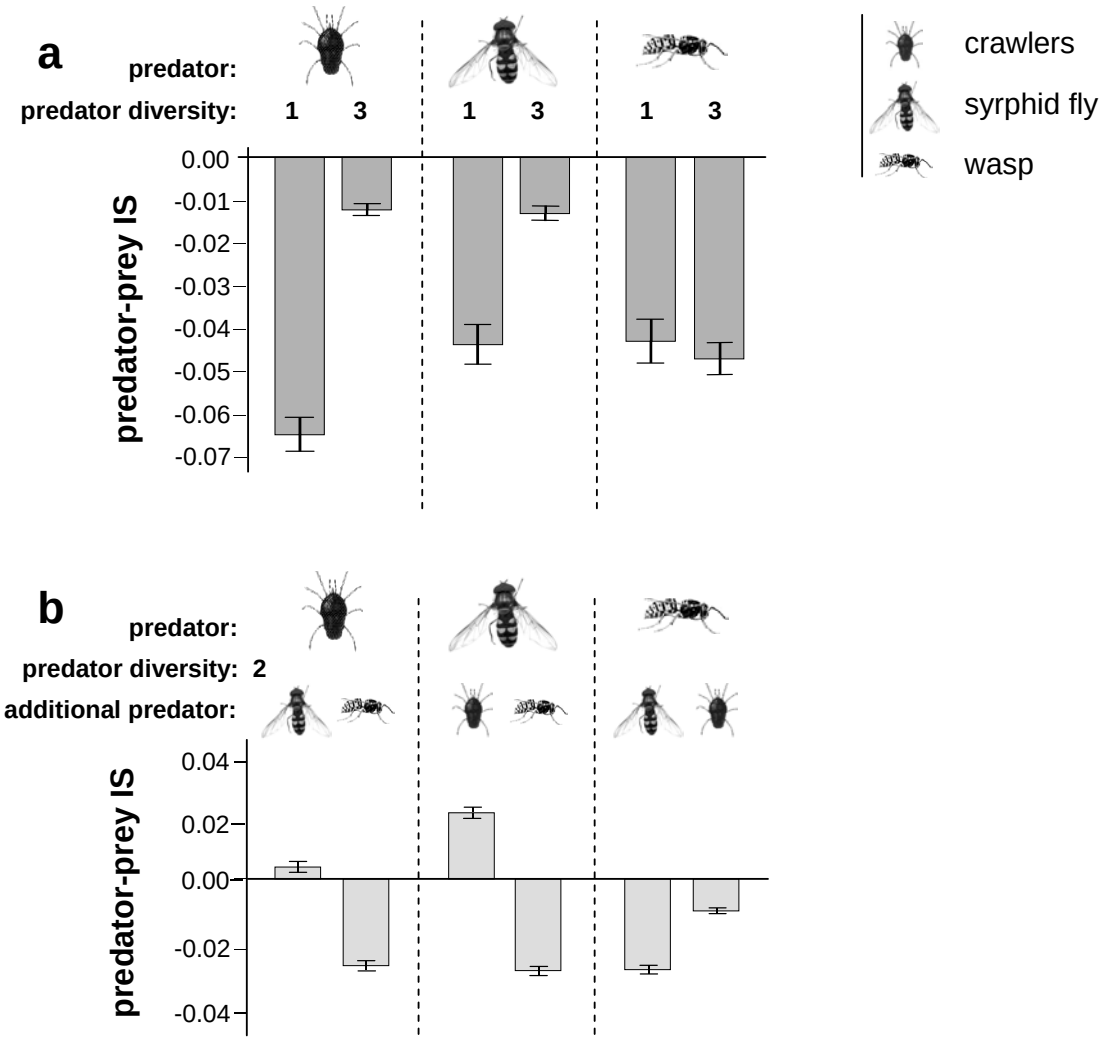


Figure 2.4 | Predator–prey interaction strength (IS, mean ± SE, bootstrapped data set; for calculation of IS see Materials and methods: Statistical analyses and interaction strengths) measured on beetle biomass at the end of the observation period. **(a)** Pairwise predator–prey IS at predator diversity levels of one (individual effects) and three (effect of predator removal from intact community); one-way ANOVA $F_{5,1994} = 32.4$, $p < 0.0001$. **(b)** Pairwise predator–prey IS at a predator diversity level of two. Each IS for each predator depends on the identity of the coexisting predator. Here, the different IS may be of similar or different algebraic signs, indicating additive (negative values) or inhibitory interactions (positive values) between the predators.

2.5 Discussion

In this study, increasing predator diversity significantly decreased herbivore biomass and average survivorship, which subsequently decreased the amount of plant biomass consumed via a trophic cascade. We did not find evidence that predator identity or a "sampling effect" drove these predator diversity effects on prey populations. Given the simplicity of the food web in our study and the trophic similarity of the predators, we hypothesized that the loss of any one of them would be compensated for by the others. However, our analyses of pairwise interaction strengths suggest that the effects of wasps on beetles was similar if it was the only predator or if it was removed from an intact predator community (diversity level 3), whereas effects were weaker when it was removed from a two predator community. This result is caused by the significant interference between the other two predators, syrphid flies and crawlers. The beetle biomass in the treatment with only syrphid flies and crawlers was much higher than in the other two-predator communities. Therefore, removing the wasp from the intact three-predator community led to a strong increase in beetle biomass, an effect which was as strong as the wasp effect when removed from a single-predator community. While effects were strong for all three predators when alone, interference between syrphids and crawlers also meant that the removal of either one from an intact predator community had much weaker effects than their removal when alone because the other one was released from interference. The removal of wasps from a two-predator community had a weaker effect compared to its removal from the three-predator community, because either the syrphids or the crawlers exerted a strong effect on the beetles prior to the wasps' appearance. Thus, strong interference between two predators (e.g., syrphids and crawlers) generated variable effects of predator diversity on pairwise interaction strengths. Interestingly, these strong non-additive interactions combined to create an overall mean diversity effect which appeared additive. As one possible mechanism for the described patterns, we propose that distinct predator phenologies determine the potential for additivity and interference among species through their influence on both temporal overlap among predators and the larval stages upon which they feed. Wasps appear later in the season than either syrphid flies or crawling predators, and they feed exclusively on third-instar beetle larvae, which increases the likelihood that their effect will be additive. Crawlers and syrphid flies have more temporal and dietary overlap with respect to beetle larval development, which may explain their significant interference and their ability to reciprocally compensate for the loss of the other. The exclusion of one of these two species thus leads to a release of interference by the other species.

Both processes, the release of interference and compensatory increases in population consumption, cause the lack of a removal effect when the other species is present. This interpretation of our results suggests that the predator identity effects on interaction strengths are driven by the phenology of predators, which results in a temporal niche separation. However, due to the low number of predator species in this community, predator identity and phenology could not be disentangled in our experiment. In particular, the wasps were the only predators with a late phenology, and other traits of the wasps that could influence the effect of their identity on interaction strengths were thus confounded with phenology. Our hypothesis, that predator phenology determines additive, compensatory, and interference effects need to be tested in a community with more predator species of varying phenology. Our results suggest that predator diversity and identity drive interaction strengths and trophic cascades when populations are not temporally well mixed. Interestingly, extrapolations of the single-species treatment effects to higher levels of predator diversity yielded expected values that were in most cases consistent with the observed values. While this could be interpreted to mean that the observed predator diversity effect was the result of changing total predator density across diversity treatments, our analyses of interaction strengths point to a combination of additivity, compensation, and interference among predators, which renders this explanation unlikely. Instead, it is likely that the variability caused by species-specific effects of predator diversity on interaction strengths generated an overall trend that appears additive. Nevertheless, we manipulated predator diversity in a field setting where all non-excluded species were allowed to vary naturally in order to explicitly investigate the consequences of biodiversity loss under natural conditions. Therefore, we cannot entirely rule out potential confounding effects of predator abundance changing with diversity levels.

Although we found a consistently strong negative effect of predator diversity on the mean herbivore biomass and the amount of plant biomass consumed, the variance among replicates was substantial. This high within-treatment variance, in effect strength, was most likely caused by the random spatial variation of detection of prey and predator nesting sites. Thus, not every trophic interaction is realized at every spatial location (Brose *et al.* 2004), which lowers average interaction strengths but increases their spatial variance (Berlow 1999). Increased variance at lower predator diversity could be due to the "sampling effect" (Ives *et al.* 2005), where one dominant predator has a strong effect, regardless of the number of coexisting predators. This hypothesis predicts that the variance in effect strength should be low in treatments in which a species with the dominant effect on herbivore or plant biomass reduction is present or absent across all replicates (Navarrete and Menge 1996). In our study system, no predator species had a dominant effect on herbivore or plant biomass

reduction – a result which is in contrast to many prior studies on predator-diversity effects on ecosystem functioning (Finke and Denno 2005, Gamfeldt *et al.* 2005, Straub and Snyder 2006). Although wasps effects were additive to other predators, they did not have a dominant effect on the beetles. This was due to the fact that wasp effects were strong in a three-predator community but not stronger than effects of other predators in the single predator or two-predator communities. Thus we conclude that predator identity did not drive the relationship between predator diversity and beetle biomass, survivorship, or herbivory.

Changes in species diversity at higher trophic levels may propagate through a food web via trophic cascades (Schmitz *et al.* 2000, Paine 2002, Shurin *et al.* 2002, Schmitz 2003). The loss of predators leads to higher herbivore abundance and thus lower plant biomass (Halaj and Wise 2001, Cardinale *et al.* 2003, Byrnes *et al.* 2006) or plant productivity (Carpenter *et al.* 1985, Duffy *et al.* 2003, Finke and Denno 2004). Yet, Shurin (2002) showed that many terrestrial trophic cascades are dampened at the herbivore-plant interface. Surprisingly, our results suggest a magnification of effects as they propagate down the food chain: when comparing the exclusion of all predators vs. the presence of all predators, the average reduction of plant biomass consumed was fifteen times larger than the reduction of beetle biomass. This may be explained by several facts. First, for building one unit of their own biomass, herbivores have to consume more than twice the amount of plant biomass, because their assimilation efficiency is less than 50% (Yodzis and Innes 1992). Second, the total plant biomass consumed includes effects of beetles that fed early and then were consumed by predators. The biomass of these beetle individuals is not included in the biomass of beetles recorded at the end of the experiment. Third, the magnification of cascading effects may be due to trait-mediated effects such that beetle larvae may feed less in the presence of predators (Krivan and Schmitz 2004, Schmitz *et al.* 2004, Byrnes *et al.* 2006). Our finding of a comparatively strong trophic cascade is consistent with recent suggestions that trophic cascades are more likely in communities with invertebrate herbivores that lack intraguild predation and in habitats with high resource availability (Borer *et al.* 2005, Finke and Denno 2005). The effect strength of a predator on plant biomass via a trophic cascade was correlated with interaction strength of the predator on the herbivorous beetles. The only exception to this pattern is that crawlers as single predators have a stronger effect on beetle biomass than on the amount of plant biomass consumed, whereas the wasps showed the opposite pattern. The crawlers consume beetle larvae of the first instar mainly. Beetles that escape predation by crawlers grow 5–50 times larger than the early instars and consequently reduce plant biomass most severely during their third instar. Additionally, we found evidence for compensatory growth of beetle individuals that escape predation. In contrast to the

crawlers, the wasps prey on late second or third instar beetle larvae and thus remove individuals with the highest maximum consumption rates. Together these facts may explain the difference between crawler effects on beetles and plants in our experiments.

2.6 Conclusions

Empirical and theoretical studies have shown that interaction strengths between species depend on species composition of the community (Berlow 1999, Brose *et al.* 2005). Therefore, the ability of any given predator to compensate for the loss of another predator depends on the composition of the remaining predator community (Straub and Snyder 2006). Consistent with these results, we found that pairwise predator–prey interaction strengths varied with predator diversity and the identity of the coexisting predators. Despite clear interference and compensation among individual predators, we observed an overall linear mean effect of predator diversity on herbivore biomass and herbivore consumption of plants. The patterns of additivity or redundancy in individual predator effects may have been driven by the phenological appearance of each predator in the food web. Interference and compensatory effects occurred between predators with a similar feeding niche, while temporally distinct predator populations may have prevented early season predators from compensating for the removal of late season predators. Thus, while predator diversity has an overall linear effect on the strength of the trophic cascade, other information about species identity was required to predict the effects of removing individual predators. If these findings generalize to more diverse food webs, phenological information along with knowledge on the food web structure (Bascompte *et al.* 2005, Brose *et al.* 2005) and species' body sizes (Emmerson and Raffaelli 2004, Brose *et al.* 2006a, b) might facilitate predictions of the consequences of predator loss in complex ecosystems.

2.7 References

Bascompte, J., C. J. Melián, and E. Salà. 2005. Interaction strength combinations and the overfishing of a marine food web. *Proceedings of the National Academy of Sciences (USA)* 102:5443–5447.

Berlow, E. L. 1999. Strong effects of weak interactions in ecological communities. *Nature* 398:330–334.

Borer, E. T., E. W. Seabloom, J. B. Shurin, K. E. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2005. What determines the strength of a trophic cascade? *Ecology* 86:528–537.

Breden, F., and M. Wade. 1985. The effect of group size and cannibalism rate on larval growth and survivorship in Plagiodera versicolora. *Entomography* 3:455–463.

Breden, F., and M. J. Wade. 1987. An experimental study of the effect of group size on larval survivorship in the imported willow leaf beetle Plagiodera versicolora (Coleoptera: Chrysomelidae). *Environmental Entomology* 16:1082–1086.

Brose, U., A. Ostling, K. Harrison, and N. D. Martinez. 2004. Unified spatial scaling of species and their trophic interactions. *Nature* 428:167–171.

Brose, U., E. L. Berlow, and N. D. Martinez. 2005. Scaling up keystone effects from simple to complex ecological networks. *Ecology Letters* 8:1317–1325.

Brose, U., *et al.* 2006a. Consumer-resource body-size relationships in natural food webs. *Ecology* 87:2411–2417.

Brose, U., R. J. Williams, and N. D. Martinez. 2006b. Allometric scaling enhances stability in complex food webs. *Ecology Letters* 9:1228–1236.

Byrnes, J., J. J. Stachowicz, K. M. Hultgren, A. R. Hughes, S. V. Olyarnik, and C. S. Thornbert. 2006. Predator diversity strengthens trophic cascades in kelp forests by modifying herbivore behavior. *Ecology Letters* 9:61–71.

Cardinale, B. J., C. T. Harvey, K. Gross, and A. R. Ives. 2003. Biodiversity and biocontrol: emergent impacts of a multiple enemy assemblage on pest suppression and crop yield in an agroecosystem. *Ecology Letters* 6:857–865.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *Bio-Science* 35:634–638.

Chang, G. C. 1996. Comparison of single versus multiple species of generalist predators for biological control. *Environmental Entomology* 25:207–212.

Duffy, J. E., J. P. Richardson, and E. A. Canuel. 2003. Grazer diversity effects on ecosystem functioning in seagrass beds. *Ecology Letters* 6:637–645.

Emmerson, M. C., and D. Raffaelli. 2004. Predator–prey body size, interaction strength and the stability of a real food web. *Journal of Animal Ecology* 73:399–409.

Finke, D. L., and R. F. Denno. 2004. Predator diversity dampens trophic cascades. Nature 429:407–410.

Finke, D. L., and R. F. Denno. 2005. Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecology Letters* 8:1299–1306.

Gamfeldt, L., H. Hillebrand, and P. R. Jonsson. 2005. Species richness changes across two trophic levels simultaneously affect prey and consumer biomass. *Ecology Letters* 8:696–703.

Halaj, J., and D. H. Wise. 2001. Terrestrial trophic cascades: how much do they trickle? *American Naturalist* 157:262–281.

Hooper, D. U., *et al.* 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75:3–35.

Hooper, D. U., and P. M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. *Science* 277:1302–1305.

Ives, A. R., B. J. Cardinale, and W. E. Snyder. 2005. A synthesis of subdisciplines: predator–prey interactions, and biodiversity and ecosystem functioning. *Ecology Letters* 8: 102–116.

Krivan, V., and O. J. Schmitz. 2004. Trait and density mediated indirect interactions in simple food webs. *Oikos* 107:239–250.

Myers, R. A., J. K. Baum, T. D. Shepherd, S. P. Powers, and C. H. Peterson. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* 315:1846–1850.

Naeem, S., and S. B. Li. 1997. Biodiversity enhances ecosystem reliability. *Nature* 390:507–509.

Naeem, S., and S. B. Li. 1998. Consumer species richness and autotrophic biomass. *Ecology* 79:2603–2615.

Navarrete, S. A., and B. A. Menge. 1996. Keystone predation and interaction strength: interactive effects of predators on their main prey. *Ecological Monographs* 66:409–429.

Paine, R. T. 2002. Trophic control of production in a rocky intertidal community. *Science* 296:736–739.

Petchey, O. L., A. L. Downing, G. G. Mittelbach, L. Persson, C. F. Steiner, P. H. Warren, and G. Woodward. 2004. Species loss and the structure and functioning of multitrophic aquatic systems. *Oikos* 104:467–478.

Petchey, O. L., and K. J. Gaston. 2002. Extinction and the loss of functional diversity. *Proceedings of the Royal Society of London Series B* 269:1721–1727.

Petchey, O. L., P. T. McPhearson, T. M. Casey, and P. J. Morin. 1999. Environmental warming alters food-web structure and ecosystem function. *Nature* 402:69–72.

Pimm, S. L., H. L. Jones, and J. Diamond. 1988. On the risk of extinction. *American Naturalist* 132:757–785.

Rank, N. E. 1994. Host-plant effects on larval survival of a salicin-using leaf beetle *Chrysomela aeneicollis* Schaeffer (Coleoptera: Chrysomelidae). *Oecologia* 97:342–353.

Rank, N. E., and J. T. Smiley. 1994. Host-plant effects on *Parasyrphus melanderi* (Diptera, Syrphidae) feeding on a Willow Leaf Beetle *Chrysomela aeneicollis* (Coleoptera, Chrysomelidae). *Ecological Entomology* 19:31–38.

Schmitz, O. J. 2003. Top predator control of plant biodiversity and productivity in an old-field ecosystem. *Ecology Letters* 6: 156–163.

Schmitz, O. J., P. A. Hamback, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *American Naturalist* 155: 141–153.

Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters* 7:153–163.

Schmitz, O. J., and L. Sokol-Hessner. 2002. Linearity in the aggregate effects of multiple predators in a food web. *Ecology Letters* 5:168–172.

Sears, A. L. W., J. T. Smiley, M. Hilker, F. Muller, and N. E. Rank. 2001. Nesting behaviour and prey use in two geographically separated populations of the specialist wasp *Symmorphus cristatus* (Vespidae: Eumeninae). *American Midland Naturalist* 145:233–246.

Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters* 5:785–791.

Smiley, J. T., and N. E. Rank. 1986. Predator protection versus rapid growth in a montane leaf beetle. *Oecologia* 70:106–112.

Smiley, J. T., and N. E. Rank. 1991. Bitterness of *Salix* along the north fork of Big Pine Creek, eastern California: species and community elevational trends. Pages 132–147 in C. A. Hall, V. Doyle-Jones, and B. Widawski, editors. Natural history of eastern California and high-altitude research, University of California. White Mountain Research Station Symposium. The Regents of the University of California, Los Angeles, California, USA.

Snyder, W. E., and A. R. Ives. 2003. Interactions between specialist and generalist natural enemies: parasitoids, predators, and pea aphid biocontrol. *Ecology* 84:91–107.

Snyder, W. E., G. B. Snyder, D. L. Finke, and C. S. Straub. 2006. Predator biodiversity strengthens herbivore suppression. *Ecology Letters* 9:789–796.

Straub, C. S., and W. E. Snyder. 2006. Species identity dominates the relationship between predator biodiversity and herbivore suppression. *Ecology* 87:277–282.

Thébault, E., and M. Loreau. 2003. Food-web constraints on biodiversity-ecosystem functioning relationships. *Proceedings of the National Academy of Sciences (USA)* 100: 14949–14954.

Tilman, D. 1996. Biodiversity: population versus ecosystem stability. *Ecology* 77:350–363.

Tilman, D. 1997. Distinguishing between effects of species diversity and species composition. *Oikos* 80:185.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80: 1455–1474.

Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379:718–720.

Vonesh, J. R., and C. W. Osenberg. 2003. Multi-predator effects across life-history stages: non-additivity of egg- and larval-stage predation in an African treefrog. *Ecology Letters* 6:503–508.

Walker, B. H. 1992. Biodiversity and ecological redundancy. *Conservation Biology* 6:18–23.

Wootton, J. T., and M. Emmerson. 2005. Measurement of interaction strength in nature. *Annual Review of Ecology, Evolution, and Systematics* 36:419–444.

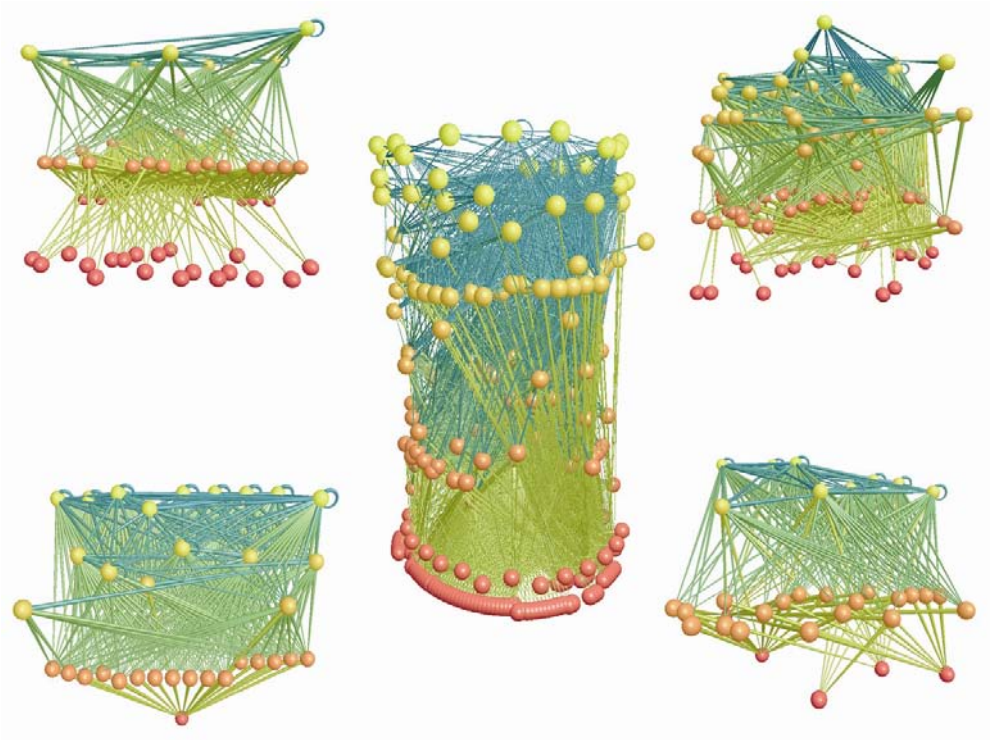
Worm, B., and J. E. Duffy. 2003. Biodiversity, productivity and stability in real food webs. *Trends In Ecology and Evolution* 18:628–632.

Yachi, S., and M. Loreau. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences (USA)* 96:1463–1468.

Yodzis, P., and S. Innes. 1992. Body size and consumer-resource dynamics. *American Naturalist* 139:1151–1175.

Chapter 3

Allometric degree distributions facilitate food-web stability



The five food webs used in the presented study. The five representations depict the trophic structure of the food webs Tuesday Lake 1984, Grand Cariçaie – ClControl2, Broadstone Stream, Skipwith Pond (clockwise, beginning at the upper left panel) and Weddell Sea Shelf (middle panel).

Food webs compiled with the help of www.foodwebs.org.

3.1 Abstract

In natural ecosystems, species are linked by feeding interactions that determine energy fluxes and create complex food webs. The stability of these food webs (De Ruiter *et al.* 2005, Montoya *et al.* 2006) enables many species to coexist and to form diverse ecosystems. Recent theory finds predator–prey body-mass ratios to be critically important for food-web stability (Emmerson *et al.* 2004, Loeuille & Loreau 2005, Brose *et al.* 2006a). However, the mechanisms responsible for this stability are unclear. Here we use a bioenergetic consumer–resource model (Yodzis & Innes 1992) to explore how and why only particular predator–prey body-mass ratios promote stability in tri-trophic (three-species) food chains. We find that this 'persistence domain' of ratios is constrained by bottom-up energy availability when predators are much smaller than their prey and by enrichment-driven dynamics when predators are much larger. We also find that 97% of the tri-trophic food chains across five natural food webs (Brose *et al.* 2005) exhibit body-mass ratios within the predicted persistence domain. Further analyses of randomly rewired food webs show that body mass and allometric degree distributions in natural food webs mediate this consistency. The allometric degree distributions hold that the diversity of species' predators and prey decreases and increases, respectively, with increasing species' body masses. Our results demonstrate how simple relationships between species' body masses and feeding interactions may promote the stability of complex food webs.

3.2 Introduction

Natural food webs are characterized by energy and biomass flows across various trophic levels. Despite the structural complexity of these large networks (Williams & Martinez 2000) simple food-chain motifs usefully represent the energy transfer (Milo *et al.* 2002, Bascompte & Melián 2005) and mechanisms responsible for non-equilibrium population dynamics in food webs (Hastings & Powell 1991, Muratori & Rinaldi 1992, Jonsson & Ebenman 1998, McCann *et al.* 1998). Analyses of food-chain motifs illustrate how population stability under chaotic dynamics may be driven by high resource productivity (Hastings & Powell 1991), variation in the species' timescales (Muratori & Rinaldi 1992) or certain body-mass ratios between consumers and resources (Jonsson & Ebenman 1998). Population persistence depends on parameters of energy gain (production and consumption) and loss (metabolism and mortality) (Gard 1980), whose rates per unit biomass follow allometric negative-quarter power-law relationships with the average body masses of the populations (Brown *et al.* 2004,

Savage *et al.* 2004). We use a bioenergetic model based on these principles (Yodzis & Innes 1992) to explore how the dynamics of top (t), intermediate (i) and basal (b) species of tri-trophic food chains changes with varying consumer–resource body-mass ratios (R). Our analyses predict the probability of stable coexistence of three invertebrate species in tri-trophic food chains depending on R, which is subsequently evaluated for food chains of five natural food webs (Brose *et al.* 2005).

3.3 Methods

Bioenergetic consumer-resource model. Population dynamics of three invertebrate species in a food chain follows a bioenergetic model (Yodzis & Innes 1992) of the biomass evolution, $\mathrm{d}B/\mathrm{d}t$, of basal (b), intermediate (i) and top (t) species:

$$dB_b / dt = r_b G_b B_b - x_i y_i F_{ib} B_i / e \,, \tag{3.1a}$$

$$dB_i / dt = -x_i B_i F_{ib} B_i - x_t y_t F_{ti} B_t / e \,, \tag{3.1b}$$

$$dB_t / dt = -x_t B_t + x_t y_t F_t B_t \,, \tag{3.1c}$$

where e is the assimilation efficiency, G_b is the logistic net growth ($G_\mathrm{b} = 1 - B_\mathrm{b}/K$) with a carrying capacity K, and F is a type II functional response [$F_\mathrm{ib} = B_\mathrm{b}/(B_0 + B_\mathrm{b})$; $F_\mathrm{ti} = B_\mathrm{i}/(B_0 + B_\mathrm{i})$] with a half saturation density B_0. Here, the fraction of the biomass removed from the resource population that is actually eaten is set to unity, which is often characterized as the mechanistically simplest model of predator–prey interactions (Jeschke *et al.* 2002). The biological rates of production (W), metabolism (X) and maximum consumption (Y) follow negative-quarter power-law relationships with the species' body masses (Brown *et al.* 2004):

$$W_b = a_r M_b^{-0.25} \,, \tag{3.2a}$$

$$X_{i,t} = a_y M_{i,t}^{-0.25} \,, \tag{3.2b}$$

$$Y_{i,t} = a_y M_{i,t}^{-0.25} \,, \tag{3.2c}$$

where a_r, a_x and a_y are allometric constants (Yodzis & Innes 1992). The timescale of the system is defined by setting the mass-specific growth rate to unity (equ. 3.3a). Then the mass-specific metabolic rates of all species, x, are normalized by the timescale (equ. 3.3b), and the maximum consumption rates, y, are normalized by the metabolic rates:

$$r_i = 1\,, \tag{3.3a}$$

$$x_{i,t} = \frac{X_{i,t}}{W_b} = \frac{a_x}{a_r}\left(\frac{M_{i,t}}{M_b}\right)^{-0.25}\,, \tag{3.3b}$$

$$y_{i,t} = \frac{Y_{i,t}}{X_{i,t}} = \frac{a_y}{a_x}\,. \tag{3.3c}$$

Substituting equations (3.3a-c) into equations (3.1a) and (3.1b) yields a population dynamic model with allometrically scaled and normalized parameters. Here the body mass of the basal species, M_b, is set to unity, and the body masses of all other species, M_i and M_t, are expressed relative to the body mass of the basal species. This makes the results presented here independent of the body mass of the basal species.

Simulations. In simulations of tri-trophic food chains, the R values between the top and intermediate species (R_{ti}) and between the intermediate and basal species (R_{ib}) define the body masses M_i and M_t. We used constant values for the other model parameters: maximum ingestion rate $y_{i,t} = 8$ for invertebrate predators; assimilation efficiency $e = 0.85$ for carnivores; carrying capacity K = 1; half saturation density of the functional response $B_0 = 0.5$; allometric constant $a = a_x/a_r = 0.2227$ (top, intermediate and bottom species were simulated as invertebrates). We sought a mechanistic explanation for the influence of R on food-web stability by simulating food chains as the simplest multitrophic motif with energy transfer across several trophic levels. This characterizes complex natural food webs better than bitrophic consumer–resource relationships. Analyses of more complex motifs such as omnivory modules require knowledge about the relative interaction strengths of generalist predators with their multiple prey, which was not available for the natural food webs studied.

We varied R between the top and intermediate species ($R_{ti} = M_t/M_i$) and between the intermediate and basal species ($R_{ib} = M_i/M_b$) between 10^{-8} and 10^{13}, which decreased their rates of metabolism (x) and consumption (xyF) per unit biomass. Simulations started with uniformly random biomass densities ($0.05 < B_{t,i,b}\ (T = 0) < 1$)

and ran more than 100,000 time steps (T) or until the largest species attained two biomass minima. We recorded the maximum and minimum biomass densities in the second half of the time series of the persistent populations ($B > 10^{-30}$) and defined a 'persistence domain' of combinations of R_{ti} and R_{ib} that enabled persistence of the three populations. For every time series we calculated the averages of the top-down pressure per unit biomass on the basal species, $P_b = x_i y_i F_{ib} B_i / B_b$, and the energy flux per unit biomass to the intermediate species, $E_i = x_i y_i F_{ib}$. Similar calculations yield the averages of the top-down pressure per unit biomass on the intermediate species and the energy flux per unit biomass to the top species.

Evaluation and re-wiring. Subsequently, we compared the R_{ti} and R_{ib} values of the persistence domain with those of all tri-trophic food chains across five natural food webs: one from a stream (Broadstone Stream), one from a pond (Skipwith Pond), one from a lake (Tuesday Lake, 1984), one terrestrial (Grand-Cariçaie, ClControl2) and one marine (Weddell Sea Shelf) from a global data base (Brose *et al.* 2005). To allow comparisons with our simulations, we studied only food chains of three invertebrate species that composed the vast majority of food chains in the empirical food webs, whereas few food chains include vertebrates or plant species. To test our hypotheses we created two additional versions of each of these empirical food webs under random and restricted re-wiring. The 'random re-wiring' algorithm conserved only the species' body masses and the total number of links, n, of the empirical food webs and randomly relinked n species pairs without any restrictions. The 'restricted re-wiring' algorithm (see Milo *et al.* 2002 and references therein) randomly selects two predator–prey pairs and reconnects the predator of the first pair with the prey of the second pair and vice versa. This re-wiring required that none of the new links already existed and ensured the conservation of the total number of predators and prey of each species along with their body masses and the total number of links in the network. We relinked n pairs of links in each food web 20 times to create a random rewired version of the network. Each of the two algorithms was applied to each of the five food webs studied with eight replicates. For each replicate we calculated the fraction of invertebrate food chains with body-mass ratios that were located within the persistence domain of our simulations under three conditions: empirical food-web structures, restricted re-wiring and random re-wiring.

Statistics. Differences in these fractions between the three versions of the food webs were statistically evaluated by eight independent Mann-Whitney U-tests. In each test the five empirical probabilities were tested against five probabilities for each re-wiring algorithm (randomly drawn from the eight replicates for each food web). Subsequently, each test was characterized by the highest of the eight p-values. The

relationships between the numbers of predator links and prey links and the body masses of the species were analysed by ordinary linear least-square regressions. Regressions were performed for each empirical replicate and one randomly rewired replicate of each of the five food webs.

3.4 Results

We initially explored a tri-trophic system by simultaneously increasing R between top and intermediate species (R_{ti}) and between intermediate and basal species (R_{ib}) from 10^{-8} to 10^{8} (that is, the consumer is between 10^{8}-fold smaller and 10^{8}-fold larger than its prey). The simultaneous increase in both R values is a simplification to gain knowledge of the population dynamics. The minima and maxima attained for the biomass densities of the three species across this range of R (Figure 3.1a-c) depict four distinct stages of coexistence. At the lowest R ($R \leq 10^{-6.7}$), the system exhibits a stable equilibrium where only the basal species persists. At higher R ($10^{-6.7} \leq R < 10^{-1.6}$), two stable attractors appear: either the basal species persists at equilibrium, or basal and intermediate species exhibit globally attractive limit cycles (Muratori & Rinaldi 1992). In this range of R, the top species is much smaller than its prey, and its mass-specific metabolic rate exceeds the energy available from consuming the intermediate species, which prevents persistence (Gard 1980). Increasing R above these low ratios decreases the metabolic rates per unit biomass of top and intermediate species and increases the intermediate species' biomass density until the top species' consumption exceeds its metabolic demand enough for the top species to persist ($R = 10^{-1.6}$). Further increases in R ($10^{-1.6} < R < 10^{3.5}$) increases top-down pressure on the intermediate species and decreases top-down pressure on the basal species (Figure 3.1d). Increasing R within this range also increases the consumption rate per unit biomass of the intermediate species over that of the top species (Figure 3.1e). This counterintuitive result is explained by the simultaneous decrease in the density of intermediate species and increase in the density of basal species, which enhances the energy availability per unit biomass to the intermediate species. This availability increases with R, leading to accelerating oscillations of top and intermediate species (Figure 3.1a-c). Mechanistically similar to the 'paradox of enrichment' (Rosenzweig 1971), the dynamics are driven from equilibrium through a series of bifurcations to more complex dynamics until the minimum density of the intermediate species drops below a critical extinction threshold, eliminating both consumer species ($R = 10^{3.5}$; Figure 3.1). The complex dynamics in this range of R are caused by the different timescales of the three populations (Muratori & Rinaldi 1992). Further increases in R

($R > 10^{3.5}$) cause unstable dynamics that continue to prevent the persistence of the intermediate and top species (Figure 3.1a-c). The persistence of all three species is thus bounded by energy availability to the top species at low R and by enrichment-driven instability of the intermediate species towards higher R.

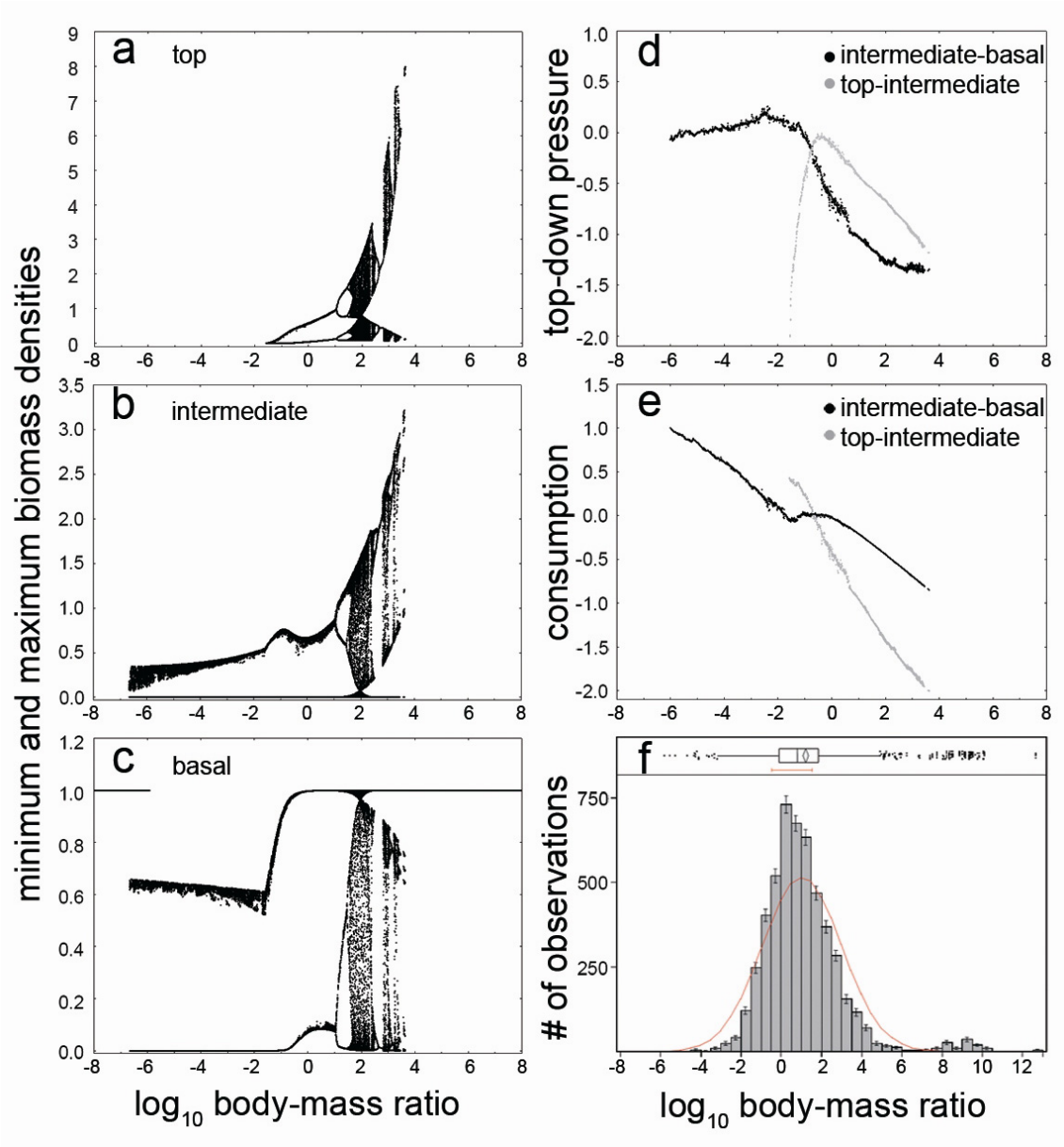


Figure 3.1 | Population dynamics in tri-trophic food chains. (a–c) Effects of R on the biomass minima and maxima of top (a), intermediate (b) and basal (c) species. **(d)** Effect of R on $\log_{10}$ of top-down pressure per unit biomass of prey, for intermediate–basal (black) and top–intermediate (grey) species. **(e)** Effect of R on $\log_{10}$ of consumption per unit biomass of predator, for intermediate–basal (black) and top–intermediate (grey) species. **(f)** Frequency distribution of empirical R in five natural food webs (means ± s.e.m.); the red line shows a normal distribution. An outlier box-plot is shown above the histogram. Simultaneous variation of R of top to intermediate and intermediate to basal species: when $R = 0$, all three species have equal size; when $R < 0$ and $R > 0$, predators are smaller and larger, respectively, than their prey.

With this mechanistic background on food-chain dynamics, we decoupled R of upper and lower trophic levels and independently varied both R_{ti} and R_{ib} between 10^{-6} and 10^{13}. This range corresponds to the range of empirical R values of the five natural food webs studied here (Figure 3.1f). In 19.6% of this parameter space, we found persistence of all three species (Figure 3.2, red areas). The energy-availability boundary of this persistence domain depends on R_{ib}, which needs to exceed a threshold ($R_{ib} > 10^{-1.6}$) within a broad range of R_{ti} ($R_{ti} > 10^{-4.3}$) to increase the density of the intermediate species (that is, the energy available) enough for the top species to persist (Figure 3.2, left boundary of red areas). If R_{ib} and R_{ti} exceed a second threshold, both top and intermediate species cease to persist as a result of enrichment-driven dynamics (Figure 3.2, right boundary of red areas). This enrichment boundary is determined more continuously and interactively by both R_{ib} and R_{ti} than the energy-availability boundary (Figure 3.2).

The persistence domain in Figure 3.2 implies that a tri-trophic food chain with R randomly chosen from the range $10^{-6} \leq R \leq 10^{13}$ has a 19.6% chance of persisting. However, 97.5 ± 4.1% (mean ± s.d.) of all invertebrate tri-trophic food chains across five natural food webs from different ecosystem types (see Methods) fall within the persistence domain (Figure 3.2a, black points; Figure 3.2d, black bars). This difference in probabilities clearly suggests that species' body-mass distributions in these food webs strongly stabilize food-chain dynamics. To further explore this hypothesis, we randomly rewired the empirical food webs in a way that preserves the body masses of the species and the total number of links while completely disrupting the food-web topology ('random re-wiring'; see Methods). An average of 81.0 ± 7.0% (mean ± s.d.) of these rewired food chains in each of the five food webs fell within the persistence domain (Figure 3.2c; 3.2d, white bars). This probability is 4.1-fold the 19.6% probability of food chains with randomly distributed body masses within empirically observed ranges that are systematically and independently linked. However, 81% is significantly lower than the 97.5% probability that empirical food chains overlap with the persistence domain ($p < 0.01$). This difference suggests that, while the distribution of species' body masses found in natural food webs provides a substantial increase in the dynamical stability of possible food chains, topological properties of actual food chains might further facilitate food-web stability. To explore which topological properties can provide this additional stabilization, we tested whether correlations between the body mass and degree of species (that is, the number of predator and prey links of a population) drive this effect. To do this, we randomly rewired the food webs with a second randomization algorithm that preserves the body mass and degree of each species ('restricted re-wiring'; see Methods). An average of 94.7 ± 6.2% (mean ± s.d.) of the food chains rewired in this restricted way lied within the

persistence domain (Figure 3.2b; 3.2d, grey bars). This probability is 4.8-fold the probability of food chains with randomly distributed body masses (19.6%) and differs significantly from randomly rewired networks (81.0%, $p < 0.05$), but it is not significantly lower than that in empirical food chains (97.5%, $p > 0.17$).

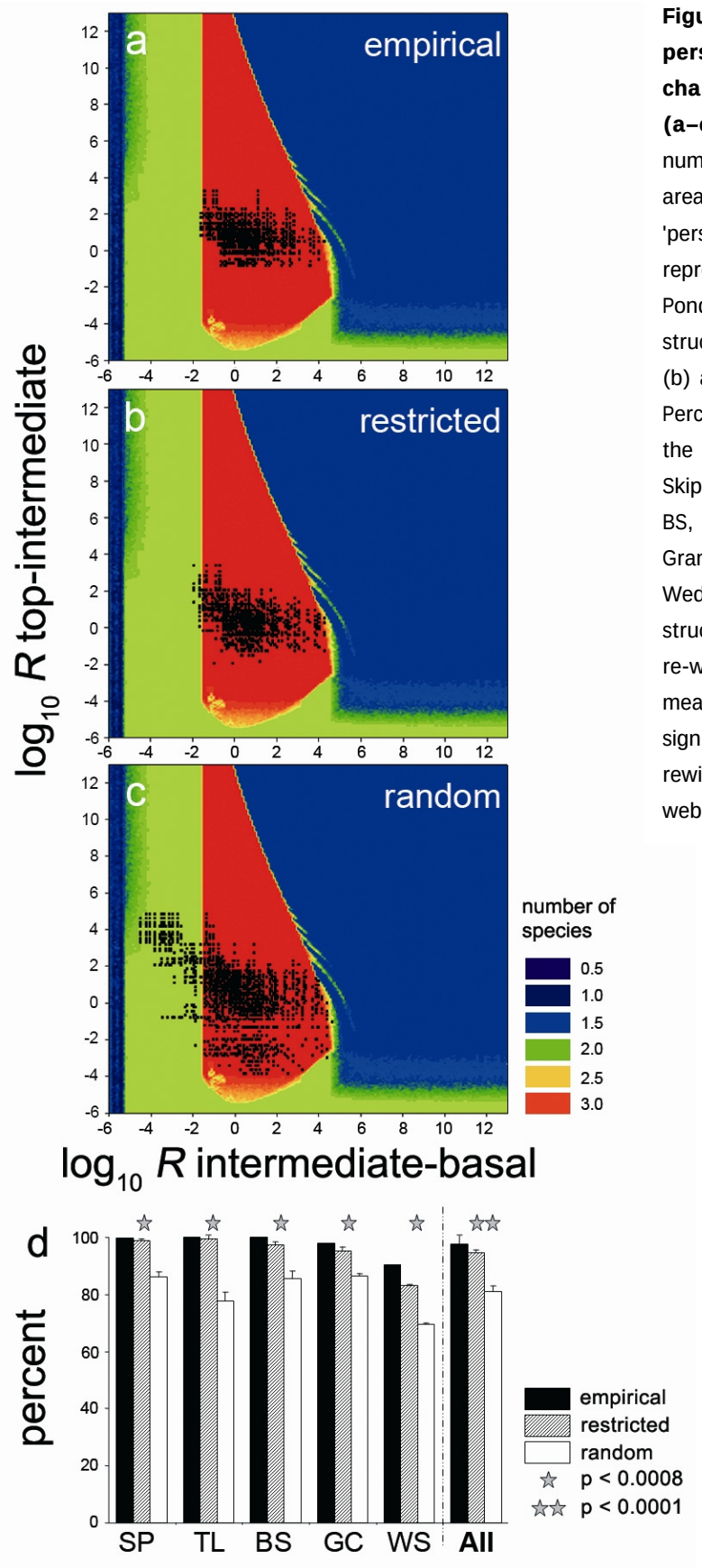


Figure 3.2 | Population persistence in tri-trophic food chains depending on R_{ti} and R_{ib}. **(a–c)** Colours indicate the numbers of persistent species; red areas characterize a tri-trophic 'persistence domain'. Black points represent food chains of Skipwith Pond under empirical food web structures (a), restricted re-wiring (b) and random re-wiring (c). **(d)** Percentages of food chains within the persistence domain (SP, Skipwith Pond; TL, Tuesday Lake; BS, Broadstone Stream; GC, Grand Cariçaie – ClControl2; WS, Weddell Sea) under empirical structures, restricted and random re-wiring; results are shown as means and s.d.; Stars indicate significant differences between the rewired versions of each food web.

3.5 Discussion

Overall, our results suggest that the distributions of and correlations between the body mass and degree of species within food webs are important mechanisms responsible for food-chain stability. Other topological properties of food webs seem to be of more minor importance. Instead, preserving allometric degree distributions realizes probabilities of tri-trophic stability similar to those found in empirical food webs. This conclusion seems qualitatively insensitive to variation in model parameters (see Supplementary Information). In the five natural food webs studied, the critically important mass–degree relationships are characterized by significant decreases in the number of predator links and significant increases in the number of prey links with increasing body masses of species (Table 3.1). These simple relationships were removed in the random procedure and retained in the restricted-re-wiring procedure (Table 3.1). Our results seem to reveal a mechanistic basis of body-mass effects on population persistence in simple tri-trophic food chains. Scaling up our analyses to complex food webs suggests that population persistence there could be determined by similar constraints (see Supplementary Information). Although domains of stability using other functional responses also need to be explored, our results for the most widely used nonlinear functional response are of broad importance to ecology. Future extensions of our approach need to also address more variation between network models, species numbers and metabolic types of species to illuminate the generality of the results described here.

Table 3.1 | Allometric degree distributions: dependence of species' link structures on body mass.

Food web	Topology	y	Regression equation	R^2	n	p
Skipwith Pond	Empirical	No. of predators	$y = -1.00\log x + 5.91$	0.21	33	0.007
		No. of prey	$y = 2.47\log x + 21.01$	0.26	33	0.003
	Random	No. of predators	$y = -0.26\log x + 9.13$	0.05	33	0.20
		No. of prey	$y = -0.08\log x + 9.94$	0.004	33	0.71
Tuesday Lake, 1984	Empirical	No. of predators	$y = -0.19\log x + 1.57$	0.47	25	0.0002
		No. of prey	$y = 0.71\log x + 12.61$	0.35	25	0.0017
	Random	No. of predators	$y = -0.03\log x + 3.50$	0.01	25	0.58
		No. of prey	$y = 0.03\log x + 4.30$	0.007	25	0.69
Broadstone Stream	Empirical	No. of predators	$y = -0.80\log x - 1.91$	0.40	29	0.0003
		No. of prey	$y = 1.44\log x + 17.76$	0.15	29	0.04
	Random	No. of predators	$y = 0.31\log x + 7.85$	0.10	29	0.10
		No. of prey	$y = -0.24\log x + 3.02$	0.10	29	0.10
Grand Cariçaie, ClControl2	Empirical	No. of predators	$y = -0.54\log x + 4.39$	0.13	102	0.0002
		No. of prey	$y = 0.61\log x + 11.59$	0.05	102	0.03
	Random	No. of predators	$y = -0.06\log x + 7.36$	0.006	102	0.45
		No. of prey	$y = -0.05\log x + 7.44$	0.004	102	0.51
Weddell Sea shelf	Empirical	No. of predators	$y = -0.44\log x + 16.93$	0.02	275	0.03
		No. of prey	$y = 1.96\log x + 20.64$	0.10	275	<.0001
	Random	No. of predators	$y = 0.04\log x + 17.68$	0.002	275	0.50
		No. of prey	$y = 0.01\log x + 17.64$	0.0003	275	0.79

Linear least-square regressions of the number of predators and prey per species (y) on the $\log_{10}$ body masses (x) of the species of five food webs under empirical food-web structures and randomly rewired networks. Empirical networks and restricted rewired networks (not shown) show similar degree distributions, because the restricted re-wiring algorithm preserves the number of predators prey per species; n is the number of invertebrate species in the food web.

Community stability is known to be critically dependent on the body-mass distribution within food webs (Emmerson & Raffaelli 2004, Loeuille & Loreau 2005, Brose *et al.* 2006a). Here we explore potential mechanisms behind these stability effects by simulating tri-trophic food chains whose persistence is possible under a limited combination of species' body masses that describe a persistence domain. These mechanisms include energy limitation of the top species when predators are much smaller than their prey and unstable enrichment-driven dynamics of intermediate species when they are much larger. Tri-trophic food chains are frequently parts of more complex motifs within food webs (Milo *et al.* 2002, Bascompte & Melián 2005) that may exhibit more stable dynamics (McCann *et al.* 1998, Fussmann & Heber 2002) or gain additional stability if large top predators couple either spatially separated food chains or other fast and slow energy channels (Koelle & Vandermeer 2005, McCann *et al.* 2005, Rooney *et al.* 2006). Although ignoring such additional model complexity the persistence domain predicted by our food-chain model is matched surprisingly well by 97.5% empirical food chains across five natural food webs. Further work on more complex food-web motifs is needed to obtain a better understanding of how body-mass-dependent population persistence scales up with system size from food chains to food webs.

3.6 Conclusions

Body masses impose physical constraints on who can hunt, handle and ingest whom in a community (Woodward *et al.* 2005, Brose 2006b), which determines the diet breadth and foraging behaviour of individual species and topological food-web parameters (Jonsson *et al.* 2005, Loeuille & Loreau 2005, Beckerman *et al.* 2006). To these relationships between body size and food webs, our study adds allometric degree distributions in which larger species feed on more prey and are consumed by fewer predators than small species. Our study provides a possible explanation for how these distributions may affect characteristics such as population persistence and food-web stability in natural communities. This connection between community-level degree distributions (Montoya & Solé 2003, Stouffer *et al.* 2005) and population biology suggests a fundamental bridge between food-web structure (Williams & Martinez 2000, Cattin *et al.* 2004, Stouffer *et al.* 2005) and food-web dynamics (Loeuille & Loreau 2005, Brose *et al.* 2006a). Our results illuminate an allometric mechanism that may help to maintain the critically important biodiversity of natural ecosystems.

3.7 Supplementary Information

In this study, we analyze the stability of tri-trophic food chains depending on varying body-mass ratios between the top and intermediate species, R_{ti}, and between the intermediate and basal species, R_{ib}. For our dynamical simulations, we use a bioenergetic model with allometrically scaling parameters (Yodzis & Innes 1992) to show how the dynamics and energetic relationships between the three species of the food chains change with varying consumer-resource body-mass ratios. Subsequently, we present (1) additional numerical simulations to provide a parameter sensitivity analysis, (2) methods of complex food-web simulations and (3) analyses of complex food webs.

3.7.1 Model sensitivity to carrying capacity and maximum consumption

The metabolic rates of the species follow allometric negative-quarter power-law relationships with the average body masses of the populations (Brown *et al.* 2004, Savage *et al.* 2004; see equ. 3.3b). The parameters of maximum consumption of the consumers, y, the carrying capacity of the basal species, K, half saturation density of the functional response, B_0 and the assimilation efficiency of the consumer species, e, are independent of the body masses, and they were assigned constant values. Following prior work (Yodzis & Innes 1992), we used an empirically supported assimilation efficiency of the consumer species of e = 0.85. The maximum per capita interaction strength of a resource species on a consumer species is proportional to y/B_0 (see McCann *et al.* 1998). In our simulations, we used constant values of the carrying capacity (K = 1), the maximum consumption of the consumers (y = 8) and the half saturation density of the functional response (B_0 = 0.5). This parameter set is consistent with simulations in previous work (Brose *et al.* 2006b). However, the shape and boundaries of the simulated 'persistence domain' (Figure 3.2a) depend on the parameters chosen (Figure 3.3a-h). Independent of the parameters used, energy limitation of the top species depends on R_{ib} whereas the boundary to unstable enrichment-driven dynamics of the intermediate species is interactively determined by both R_{ib} and R_{ti}. Increasing the carrying capacity, K (Figure 3.3a-d), is equivalent to increasing the enrichment of the food chains, which leads to a decreasing size of the persistence domain (Figure 3.3a-d). Increasing the maximum consumption rate, y, causes higher top down pressure by the consumer species, but the effects on the size of the persistence domain are marginal (Figure 3.3e-h). Note that y equal to one represents a system in which the maximum ingestion rate is equal to the metabolic rate of the consumer. The energy gain by consumption is given by the product of

consumption rate and assimilation efficiency (e = 0.85). Moreover, at prey densities below infinity, the actual consumption rate is lower than the possible maximum consumption rate.

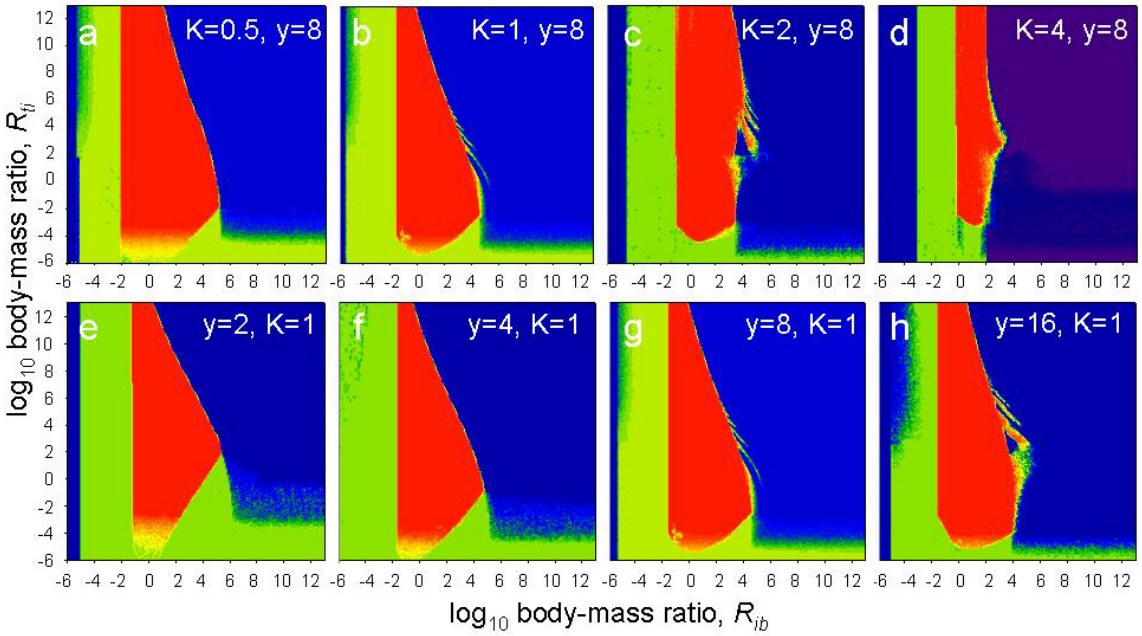


Figure 3.3 | The size and shape of the 'persistence domain' (red areas) depend on **(a-d)** the carrying capacity of the system, K (here with constant y = 8), but varies only marginally with **(e-h)** the maximum ingestion rate of the consumers, y (here with constant K = 1).

Therefore, systems with a maximum consumption rate of unity are not feasible (Figure 3.4b). Variation in K is equivalent to variation of the enrichment of the food chain and variation of the maximum ingestion rate alters the maximum per capita interaction strength (y/B_0). As increasing y is qualitatively similar to decreasing B_0, we only varied y in our additional simulations.

The percentages of empirical and re-wired food chains within the persistence domain also depend on K and y (Figure 3.4a, b). However, our general result, that food-chain stability in empirical food webs and under restricted re-wiring is significantly higher than food-chain stability under random re-wiring of the network structures, holds across the range in K and y in our simulations. For $K > 4$ all food chains are unstable due to too large enrichment (Figure 3.4a).

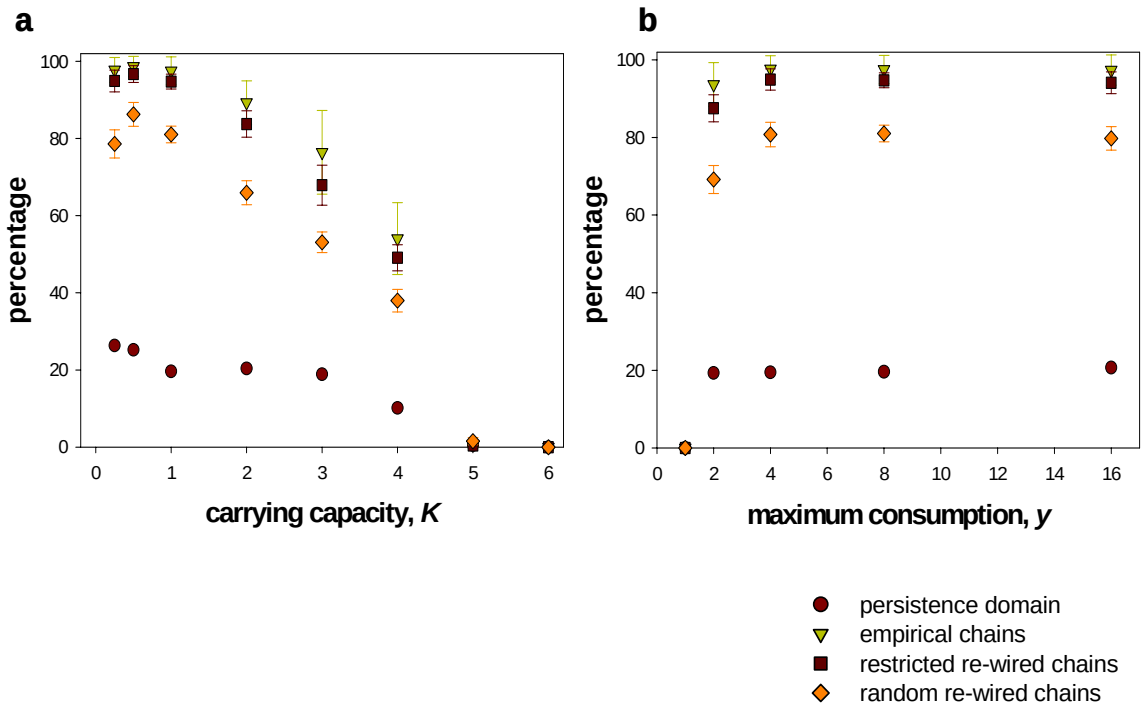


Figure 3.4 | The size of the 'persistence domain' (circles, i.e., red areas of Figure 3.2) depends on **(a)** the carrying capacity of the system, K and **(b)** the maximum ingestion rate of the consumers, y. The number of persistent empirical (triangles) and re-wired food chains (restricted: squares, random: diamonds) falling in the persistence domain (i.e., black points in Figure 3.2) also depends on these parameters. Shown are the mean and 95% confidence intervals.

3.7.2 Complex food-web analyses – Methods

Additionally to the food-chain analyses, we simulated niche-model food webs (Williams & Martinez 2000) (100 replicates per body-mass ratio) with a species richness of 20 (thereof 5 basal species) and a connectance of 0.15. The trophic level of a species i is calculated as the prey-averaged trophic level T_i:

$$T_i = 1 + \frac{\sum_{j=1}^{n} T_j}{n} \qquad (3.4)$$

where i has n prey species j. In complex food webs with constant predator-prey body-mass ratios, Z, the body masses of basal species are set to unity and the body masses of consumers, M_i, increase with their trophic levels by:

$$M_i = Z^{T_j - 1}. \qquad (3.5)$$

These body masses are used to parameterize the metabolic rates of the bioenergetic model. Thus, knowledge on the trophic levels of the species from the binary feeding matrix predicted by the niche model allows calculating their body masses relative to the body mass of the producer species (equ. 3.4), which parameterizes the parameters of the consumer-resource model (equ. 3.1a-c). We used constant values for the other model parameters: maximum ingestion rate y = 8 for invertebrate predators; assimilation efficiency e = 0.85 for carnivores; carrying capacity K = 1; half saturation density of the Holling Type II functional response B_0 = 0.5; allometric constant a = 0.2227 when all species are invertebrates. After simulations over 250,000 time steps, we calculated the fraction of persistent species ($B > 10^{-30}$). We started every individual simulation with a food web stochastically generated by a specific model initialized with uniformly random population densities in terms of biomass density of species i ($0.05 < B_i < 1$) and recorded the number of persistent populations ($B_i > 10^{-30}$) at the end of the time series (t = 250,000). Note that: (i) simulations with shorter time series (e.g., t = 50,000) would yield qualitatively similar results with a slightly higher proportional persistence but would not allow to analyse the dynamics of very large consumer-resource body-mass ratios; and (ii) different extinction thresholds produce qualitatively the same results at different levels of persistence (lower extinction thresholds increase the persistence). We measured the

fraction of persistent populations (i.e., species richness persisting at the end of the simulation divided by initial species richness) and the maximum trophic level in the food web (i.e., the maximum of the trophic levels of the populations in the food web).

3.7.3 Complex food-web analyses – Results

Consistent with the food chain analyses, population persistence in 20-species food-web models first increases and then decreases with predator-prey body-mass ratios, *R* (Figure 3.5a). A prior study (Brose *et al.* 2006a) that averaged results over varying functional responses, network models, species numbers and metabolic types of species found only the increasing population persistence with *R* of this hump-shaped relationship. This may partially be explained by the fact that networks of higher species richness or those comprised of vertebrate species continue increasing in persistence up to higher body-mass ratios than the 20-species food webs of invertebrates addressed in the present studies. Future studies need to analyze these differences. Despite these quantitative differences, the model presented here addressed the mechanistic basis of body-mass effects on population persistence. Moreover, our results suggest a hump-shaped relationship between the maximum trophic level in the food web and the predator-prey body-mass ratio: maximum trophic levels first increase and then decrease with increasing *R* in our simulations (Figure 3.5b). A plateau of maximum trophic levels is reached between body-mass ratios of 10^{-1} and 10^{2}. In this range of *R* the average of the maximum trophic level (i.e., the average over 100 niche-model food webs) does not significantly differ from three (i.e., three is within the 95% confidence intervals, Figure 3.5b). This suggests that food chains in these simulated food webs may include up to three species, whereas simulated food webs with lower or higher body-mass ratios are restricted to shorter food chains. This suggests that tri-trophic food chains might be restricted to intermediate body-mass ratios in complex food webs, which is consistent with our conclusion in the main text of the manuscript.

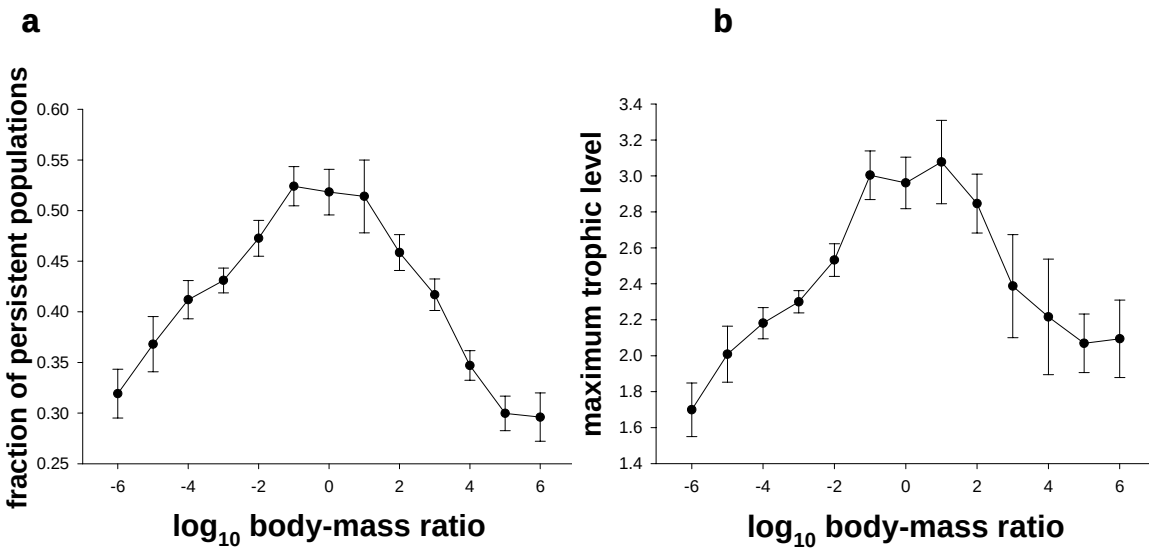


Figure 3.5 | Analyses of complex niche-model food webs: **(a)** The fraction of initial populations that dynamically persist and **(b)** the maximum trophic level amongst the persistent populations depending on the predator-prey body-mass ratios in the food webs. Data points are means and 95% confidence intervals over 100 niche-model food webs of 20 species.

3.8 Analytical Solution – Isosurfaces

To study the tri-trophic food chain analytically, we assume equilibrium biomass densities of all three species ($dB_{b,i,t}/dt = 0$). Solving the three equations of our population-dynamic model (equ. 3.1a-c) under equilibrium assumptions for B_i^* yields three different isosurfaces. The isosurface for the basal species ($dB_b/dt = 0$) is given by

$$B_i^* = \frac{e\left(-B_b^* + K\right)\left(B_b^* + B_0\right)}{x_i y_i K}, \qquad (3.6a)$$

the intermediate species' isosurface ($dB_i/dt = 0$) by

$$B_i^* = \frac{ex_i B_0 B_b^* + ex_i B_0^2 - ex_i y_i B_0 B_b^* + x_t y_t B_b^* B_t^* + x_t y_t B_0 B_t^*}{ex_i\left(y_i B_b^* - B_b^* - B_0\right)}, \qquad (3.6b)$$

and the top species' isosurface ($dB_t/dt = 0$) by

$$B_i^* = \frac{B_0}{y_t - 1}. \tag{3.6c}$$

Figure 3.6 shows the three isosurfaces in the basal-intermediate-top phase space. The feasibility of three-species food chains requires that the isosurfaces of all three species intersect in the positive phase space ($B_b > 0$; $B_i > 0$; $B_t > 0$). If the condition

$$y_i \leq -\frac{B_0 + K}{B_0 - K} \tag{3.7}$$

is satisfied, the feasibility boundary is given by

$$x_{i(f)} = -\left(\frac{e(B_0 + K - y_i K)(y_t - 1)}{K(y_i - 1)^2} \right), \tag{3.8}$$

where $x_{i(f)}$ is the metabolic rate of the intermediate species at the feasibility boundary (Figure 3.6a). If the condition of equation (3.7) does not hold, the feasibility boundary is given by

$$x_{i(f)} = \frac{e(B_0 + K)^2 (y_t - 1)}{4 y_i K B_0} \tag{3.9}$$

(see Figure 3.6b). Both equations 3.8 and 3.9 suggest that the feasibility of the three-species food chain depends on the assimilation efficiency, e, the half saturation density of the functional response, B_0, the maximum ingestion rate, y, the carrying capacity, K, and the metabolic rate of the intermediate species, x_i. However, the feasibility does not depend on the metabolic rate of the top species, x_i. Interestingly, this suggests that the feasibility of the food chain depends on the body-mass ratio between the intermediate and the basal species – that determines x_i (see equ. 3.3b) – whereas it does not depend on the body-mass ratio between the top and the intermediate species

– that determines x_t. This result is consistent with the numerical results (see Figure 3.2).

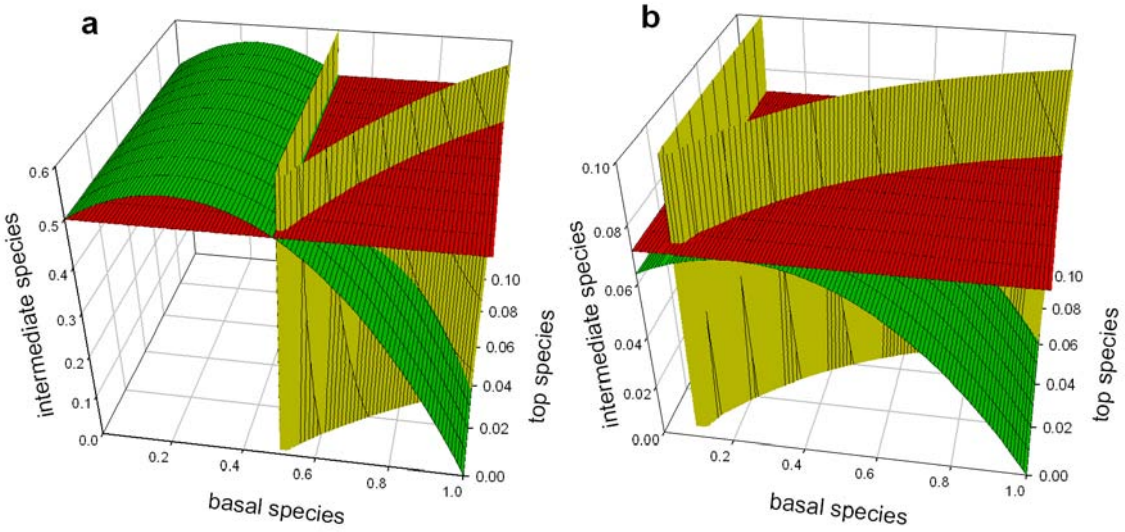


Figure 3.6 | Phase-space diagrams with isosurfaces of the top (red), intermediate (yellow) and basal (green) species of a tri-trophic food chain (equ. 3.6a-c). **(a)** isosurfaces with $y_{i,t}$ = 2 at the feasibility boundary ($R \approx$ -1.2; see equ. 3.8). **(b)** isosurfaces with $y_{i,t}$ = 8 at the feasibility boundary ($R \approx$ -2.3; see equ. 3.9).

3.9 References

Bascompte, J. & Melià n, C. J. Simple trophic modules for complex food webs. *Ecology* 86, 2868–2873 (2005).

Beckerman, A. P., Petchey, O. L. & Warren, P. H. Foraging biology predicts food web complexity. *Proc. Natl Acad. Sci. USA* 103, 13745–13749 (2006).

Brose, U. et al. Body sizes of consumers and their resources. *Ecology* 86, 2545 (2005).

Brose, U., Williams, R. J. & Martinez, N. D. Allometric scaling enhances stability in complex food webs. *Ecol. Lett.* 9, 1228–1236 (2006a).

Brose, U. et al. Consumer–resource body-size relationships in natural food webs. *Ecology* 87, 2411–2417 (2006b).

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. Toward a metabolic theory of ecology. *Ecology* 85, 1771–1789 (2004).

Cattin, M. F., Bersier, L. F., Banašek-Richter, C., Baltensperger, R. & Gabriel, J. P. Phylogenetic constraints and adaptation explain food-web structure. *Nature* 427, 835–839 (2004).

De Ruiter, P. C., Wolters, V., Moore, J. C. & Winemiller, K. O. Food web ecology: Playing Jenga and beyond. *Science* 309, 68–70 (2005).

Emmerson, M. C. & Raffaelli, D. Predator–prey body size, interaction strength and the stability of a real food web. *J. Anim. Ecol.* 73, 399–409 (2004).

Fussmann, G. F. & Heber, G. Food web complexity and chaotic population dynamics. *Ecol. Lett*. 5, 394–401 (2002).

Gard, T. C. Persistence in food webs: Holling type II food chains. *Math. Biosci.* 49, 61–67 (1980).

Hastings, A. & Powell, T. Chaos in a three-species food chain. *Ecology* 72, 896–903 (1991).

Jeschke, J. M., Kopp, M. & Tollrian, R. Predator functional responses: Discriminating between handling and digesting prey. *Ecol. Monogr.* 72, 95–112 (2002).

Jonsson, T. & Ebenman, B. Effects of predator–prey body size ratios on the stability of food chains. *J. Theor. Biol.* 193, 407–417 (1998).

Jonsson, T., Cohen, J. E. & Carpenter, S. R. Food webs, body size, and species abundance in ecological community description. *Adv. Ecol. Res* 36, 1–84 (2005).

Koelle, K. & Vandermeer, J. Dispersal-induced desynchronization: from metapopulations to metacommunities. *Ecol. Lett.* 8, 167–175 (2005).

Loeuille, N. & Loreau, M. Evolutionary emergence of size-structured food webs. *Proc. Natl Acad. Sci. USA* 102, 5761–5766 (2005).

McCann, K., Hastings, A. & Huxel, G. R. Weak trophic interactions and the balance of nature. *Nature* 395, 794–798 (1998).

McCann, K. S., Rasmussen, J. B. & Umbanhowar, J. The dynamics of spatially coupled food webs. *Ecol. Lett.* 8, 513–523 (2005).

Milo, R. *et al.* Network motifs: Simple building blocks of complex networks. *Science* 298, 824–827 (2002).

Montoya, J. M. & Solé, R. V. Topological properties of food webs: from real data to community assembly models. *Oikos* 102, 614–622 (2003).

Montoya, J. M., Pimm, S. L. & Solé, R. V. Ecological networks and their fragility. *Nature* 442, 259–264 (2006).

Muratori, S. & Rinaldi, S. Low- and high frequency oscillations in three-dimensional food chain systems. *SIAM J. Appl. Math.* 52, 1688–1706 (1992).

Rooney, N., McCann, K., Gellner, G. & Moore, J. C. Structural asymmetry and the stability of diverse food webs. *Nature* 442, 265–269 (2006).

Rosenzweig, M. L. Paradox of enrichment: destabilization of exploitation of ecosystems in ecological time. *Science* 171, 385–387 (1971).

Savage, V. M., Gillooly, J. F., Brown, J. H., West, G. B. & Charnov, E. L. Effects of body size and temperature on population growth. *Am. Nat.* 163, E429–E441 (2004).

Stouffer, D. B., Camacho, J., Guimera, R., Ng, C. A. & Amaral, L. A. N. Quantitative patterns in the structure of model and empirical food webs. *Ecology* 86, 1301–1311 (2005).

Williams, R. J. & Martinez, N. D. Simple rules yield complex food webs. *Nature* 404, 180–183 (2000).

Woodward, G. *et al.* Body size in ecological networks. *Trends Ecol. Evol.* 20, 402–409 (2005).

Yodzis, P. & Innes, S. Body size and consumer–resource dynamics. *Am. Nat.* 139, 1151–1175 (1992).

Chapter 4

Body mass, diversity and network structure drive food-web robustness against species loss

Calvin & Hobbes. The six year old Calvin imagines his stuffed tiger as his best friend. They often discuss serious and philosophical questions, peppered with a punch line. © by Bill Watterson

4.1 Abstract

Scientists urgently need to better understand how the current catastrophic loss of species directly due to human activities may further accelerate indirect losses of biodiversity in complex natural ecosystems. We explore such interdependence by simulating the nonlinear population dynamics resulting from eliminating consumer species within nine complex natural food webs. We find that the risk of "secondary" species loss due to "primary" species loss depends on characteristics of the species initially lost and the food webs within which they interact. Food webs with low species diversity and a high number of basal species are most robust against secondary extinctions. At the species level, we found the highest robustness following loss of species with low body masses, high trophic levels and low generality. This suggests that primary extinctions of large, generalist consumer species at low trophic levels in diverse food webs with few basal species are most likely to trigger cascades of secondary extinctions within ecological communities. Together, these findings offer new opportunities for understanding and predicting the sensitivity of ecosystems and their services to species loss.

4.2 Introduction

One of the most challenging and critically important scientific questions concerns the effects of rapid species loss on natural ecosystems. This loss includes both one of the largest and fastest waves of extinctions since life established on Earth (Pimm *et al.* 1995, Salà *et al.* 2000) and also the loss of species' populations at rates much higher than current extinction rates (Hughes *et al.* 1997). Such losses can trigger a cascade of further species loss (Paine 1966, Power *et al.* 1996, Srinivasan *et al.* 2007) and greatly alter the stability and functioning of ecosystems (Luck *et al.* 2003). To understand and predict ecological effects of species loss, we need to know which and how species loss causes further losses of biodiversity in natural ecosystems (De Ruiter *et al.* 2005). Studies find that properties of food webs (i.e., networks of species linked by feeding interactions) and characteristics of species initially lost help elucidate this crucial question (Pimm 1980, Borrvall *et al.* 2000, Solé & Montoya 2001, Dunne *et al.* 2002, Ebenman *et al.* 2004, Thébault *et al.* 2007). However, the small size, minimal complexity, or lack of dynamics of the systems explored in studies limit the degree to which answers may apply to naturally large, complex and dynamic ecosystems.

Early linear stability analyses of small food-web modules (Pimm 1979, 1980) suggest that food-web robustness against secondary extinctions, hereafter, "robustness", decreases with increasing species richness of food webs, hereafter,

"diversity". This is expected based on negative diversity-stability relationships found in similar analyses of random interaction networks (May 1972). In contrast, recent extensions of such analyses suggest that robustness increases with increasing species diversity within functional groups and increasing trophic position of the species initially removed (Borrvall *et al.* 2000, Ebenman *et al.* 2004). These discrepancies may be caused by the presence (Borrvall *et al.* 2000) or absence (Pimm 1979, 1980) of intraspecific competition in the studies (Thébault *et al.* 2007). While such dynamical analyses focus on small food-web modules, several structural analyses ignore population dynamics and top-down effects while focusing on bottom-up effects in whole natural food webs with high diversity (Solé & Montoya 2001, Dunne *et al.* 2002, Srinivasan *et al.* 2007). By analyzing secondary extinctions that occur only when a species looses all of its prey, these analyses find that robustness is independent of diversity (Dunne *et al.* 2002), decreases with the number of links to the species removed (Solé & Montoya 2001, Dunne *et al.* 2002) and increases with connectance (Dunne *et al.* 2002).

The contradictions and limitations of these studies leave much to be resolved by combining and enhancing the different approaches. Recent advances integrated the structure of large complex food webs with allometrically parameterized models of population dynamics and found that high predator-prey body-mass ratios are critical for food-web stability (Emmerson & Raffaelli 2004, Loeuille & Loreau 2005, Brose *et al.* 2006b). In particular, large consumers of small bodied species at low trophic levels appear to be especially important for food-web stability (Otto *et al.* 2007). Here, we extend these approaches and integrate structural and dynamical methods to analyze secondary extinctions following removal of consumer species from models of nine natural food webs parameterized with the empirical feeding relationships and body masses of the species found in those food webs. We test several hypotheses including whether or not the removed species' body mass (Brose *et al.* 2006b), trophic level (Borrvall *et al.* 2000, see also Ebenman *et al.* 2004, Thébault *et al.* 2007) or connectedness (Solé & Montoya 2001, Dunne *et al.* 2002) strongly affects food-web robustness by analyzing our data set with and also without assuming explicit intraspecific competition amongst predators (in regard to Thébault *et al.* 2007).

4.3 Methods

We explore food-web robustness by simulating species loss within nine empirical food webs. Therefore, we exclude one consumer species ('species excluded', hereafter *SE*) at the first time step of each simulation and repeat this independently for each consumer species in each food web. The analyses are replicated once under the assumption of predator interference, and once without. After species removal, other populations of species go extinct if their biomass densities fall below a critical extinction threshold ($B_i < 10^{-30}$). We define food-web robustness (R) as the fraction of initial species that persist after species removal: $R = (S_p / S_i)$, where S_p and S_i are the number of persistent and initial species (excluding *SE*), respectively.

Population dynamics. We use a bioenergetic consumer-resource model (Yodzis & Innes 1992) to describe the change of biomass over time, B'_i, of i-th autotroph producer species (equ. 4.1a) and i-th heterotroph consumer species (equ. 4.1b) in an n-species system:

$$B'_i = r_i(M_i)G_iB_i - \sum_{j=consumers}^{n} \frac{x_j(M_j)y_jB_jF_{ji}(B)}{e_{ji}f_{ji}}, \quad (4.1a)$$

$$B'_i = -x_i(M_i)B_i + \sum_{j=resources} x_i(M_i)y_iB_iF_{ij}(B) - \sum_{j=consumers} \frac{x_j(M_j)y_jB_jF_{ji}(B)}{e_{ji}}. \quad (4.1b)$$

For each species i, B_i is its biomass, r_i is its mass-specific maximum growth rate, M_i is its average body mass, G_i is its logistic net growth ($G_i = 1 - B_i / K$) with a carrying capacity K, x_i is its mass-specific metabolic rate, y_i is its maximum consumption rate relative to its metabolic rate, and e_{ji} is the assimilation efficiency of population j consuming population i. F_{ij} describes the fraction y_i that is realized when consuming j:

$$F_{ij} = \frac{\Omega_{ij}B_j}{B_0 + cB_i + \sum_{k=resources}\Omega_{ik}B_k}, \quad (4.2)$$

where B_0 is the density of prey at which species i attains half of its maximum consumption rate, Ω_{ij} is the proportion of y_i targeted to consuming j, and c describes predator interference (Beddington 1975, De Angelis *et al.* 1975). The predator-interference term in the denominator quantifies the degree to which individuals within

population *i* interfere with one another's consumption activities, which reduces *i*'s per capita consumption if $c > 0$. We used uniform relative consumption rates for consumers with n resources ($\Omega_{ij} = 1/n$) – that is, consumers do not have an active resource preference, but rather feed according to the relative biomasses of their resource species.

The biological rates of production, W, metabolism, X, and maximum consumption, Y, follow negative-quarter power-law relationships with the species' body masses (Enquist *et al.* 1999, Brown *et al.* 2004):

$$W_P = a_r M_P^{-0.25}, \tag{4.3a}$$

$$X_C = a_x M_C^{-0.25}, \tag{4.3b}$$

$$Y_C = a_y M_C^{-0.25}, \tag{4.3c}$$

where a_r, a_x and a_y are allometric constants and C and P indicate consumer and producer parameters, respectively (Yodzis & Innes 1992). The time scale of the system is defined by normalizing the biological rates by the mass-specific growth rate of the smallest producer species P^*. Then, the maximum consumption rates, Y_C, are normalized by the metabolic rates, X_C:

$$r_i = \frac{W_P}{W_{P^*}} = \left(\frac{M_P}{M_{P^*}}\right)^{-0.25}, \tag{4.4a}$$

$$x_i = \frac{X_C}{W_{P^*}} = \frac{a_x}{a_r}\left(\frac{M_C}{M_{P^*}}\right)^{-0.25}, \tag{4.4b}$$

$$y_i = \frac{Y_C}{X_C} = \frac{a_y}{a_x}. \tag{4.4c}$$

Substituting equations 4.4a-c into equations 4.1a-b yields a population-dynamic model with allometrically scaled and normalized parameters. We used constant values for the following model parameters: predator interference $c = 0$ for simulations without interference, $c = 1$ for simulations with interference; maximum ingestion rate $y_j = 4$ for vertebrates, $y_i = 8$ for invertebrate predators; assimilation efficiency $e_{ij} = 0.85$ for

carnivores and e_{ij} = 0.45 for herbivores; carrying capacity K = 1; half saturation density of the functional response B_0 = 0.5; allometric constants a_x/a_r = 0.314 for invertebrates and a_x/a_r = 0.88 for ectotherm vertebrates. Independent simulations of each food web started with uniformly random initial biomass densities ($0.05 < B_i < 1$), and run for 30 years as calculated by inserting M_P^* in (3a) and taking the inverse of W_P^* [1/years]. Basal species were not removed from the web nor allowed to decrease below one tenth of their carrying capacity to prevent their extinction and maintain them as an energy source of the food web. Structural and metabolic parameters were set using nine natural food webs of high taxonomic resolution for which body-mass data was available (Table 4.1). These marine, freshwater and terrestrial food webs contain variable numbers of ectotherm and endotherm vertebrate and invertebrate species.

Statistics. We found a significant block effect of food-web identity on robustness (ANOVA, $F_{8,387}$ = 2388.3, $p < 0.0001$). Significant differences in robustness between food webs (i.e., identity effects) are analyzed with five food-web parameters (diversity, number of basal species, connectance, omnivory and average trophic level of species) as independent variables in stepwise Reduced Major Axis regressions (RMA). Unlike least squares statistics, RMAs avoid effects of potential measurement errors in the independent variables. RMAs provide correlation coefficients to quantify the strength of the relationship and 95% confidence limits of the slope that is statistically significant if zero is outside those limits. Stepwise RMAs choose the independent variable with the strongest correlation with the dependent variable, save the residuals and subsequently conduct residual-based RMAs on the remaining parameters in the next step until no significant effects remain. This procedure is independently repeated for interference and non-interference data. To exclude the block effect of food-web identity from further analyses at the species level, we standardized all independent and dependent variables to zero mean and unit variance for each food web independently. This normalisation yields species' level parameters that scale relative to the food-web average of the parameter. Stepwise RMAs identify the dependencies of robustness on $\log_{10} SE$ body mass (hereafter: body mass) and three characteristics of the local network environment of the SE – its trophic level, vulnerability (number of predators), and generality (number of prey). This procedure is independently repeated for interference and non-interference data.

4.4 Results

In simulations with predator interference, food-web robustness against secondary extinctions decreases with increasing species diversity (Fig. 4.1a). In stepwise reduced major axis regressions (RMA), diversity is the independent community parameter with the strongest correlation that explained 70% of the variation in robustness. The analysis reveals that the residuals of the robustness-diversity relationship are strongly and positively correlated with the number of basal species in the food webs (Fig. 4.1b). Together, these two independent variables explain 95% of the across community variation in robustness. Additional residual analyses on the remaining unexplained variation by stepwise RMA shows that robustness increases with increasing connectance (Fig. 4.1c) and an increasing average trophic level within the food webs (Fig. 4.1e), whereas it decreases with increasing average omnivory of the consumers in the food webs (Fig. 4.1d). Results for food-web simulations without predator interference are similar, except for a weak negative effect of increasing connectance on food-web robustness (data not shown). Overall, these analyses identify trends in robustness across food webs, suggesting that communities with a high diversity but few basal species are most sensitive to primary extinctions.

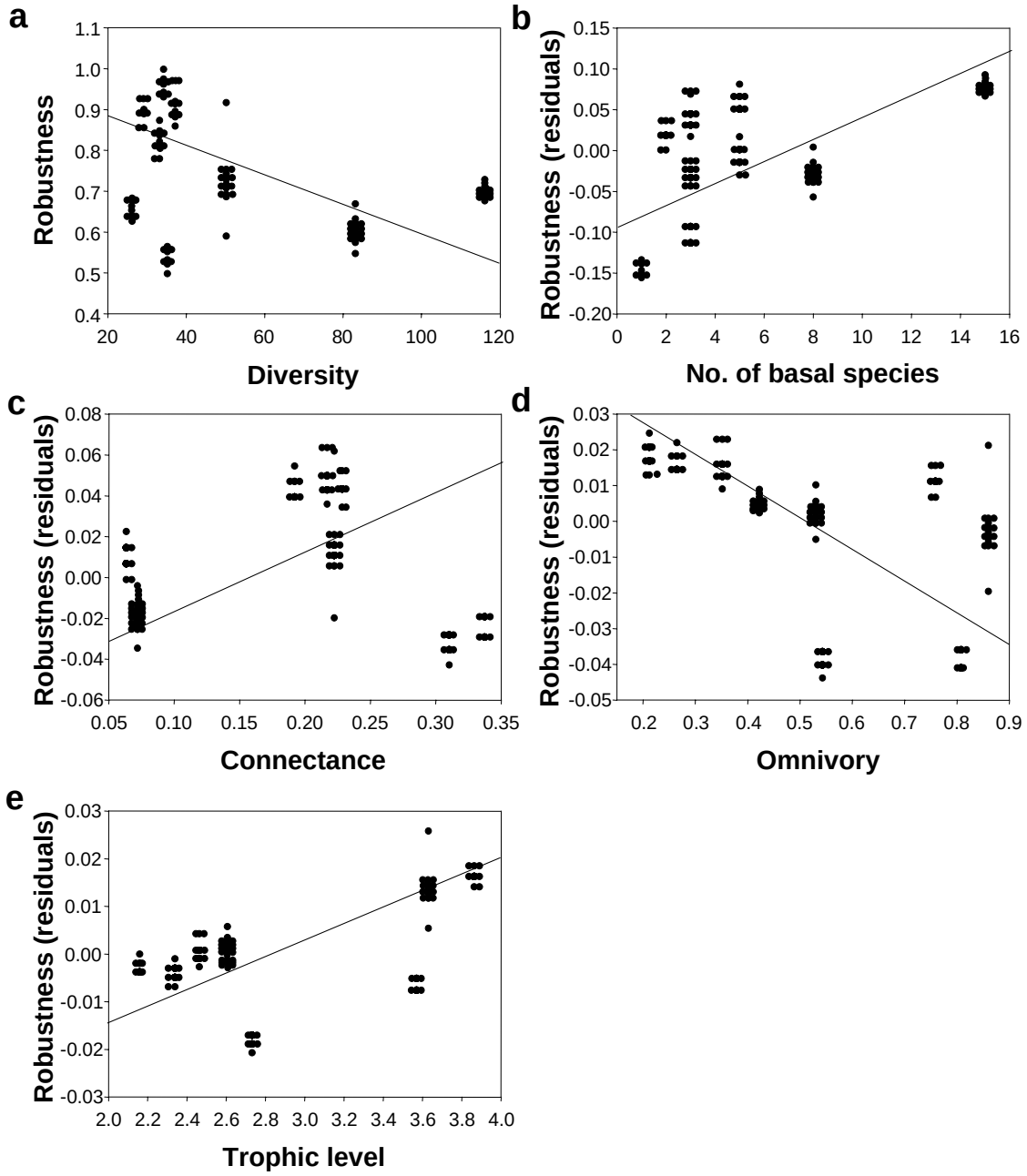


Figure 4.1 | Effects of food-web parameters on robustness. Stepwise RMA of robustness depending on **(a)** food-web diversity, correlation value c = -0.4, slope = -0.004 (lower 95% CL = -0.005, upper 95% CL = -0.003), intercept = 0.96, R^2 = 0.70; **(b)** initial number of basal species, c = 0.68, slope = 0.01 (0.01, 0.02), intercept = -0.09, R^2 = 0. 84; **(c)** connectance, c = 0.21, slope = 0.29 (0.18, 0.48), intercept = -0.05, R^2 = 0.61; **(d)** average omnivory, c = -0.50, slope = -0.09 (-0.10, -0.07), intercept = 0.05, R^2 = 0.75 and **(e)** average trophic level, c = 0.58, slope = 0.02 (0.01, 0.02), intercept = -0.05, R^2 = 0.79. Data and analyses based on simulations with predator interference. Note: Robustness of (b)-(e) represents residuals of prior analyses (see Methods regarding stepwise RMAs). Offset of multiple data points for better determination of parameter effects on robustness.

After removing the effects of food-web identity by data normalisation (see Methods), we continue our stepwise RMA analyses at the species level to identify which species losses are most likely to cause cascades of secondary extinctions. In the data set with predator interference, standardized robustness is most strongly correlated with SE ('species excluded') $\log_{10}$body mass. This negative relationship explains 59% of the variation (Fig. 4.2a). Subsequent residual analyses show that standardized robustness against secondary extinctions increases with the trophic level of the species initially excluded (Fig. 4.2b), whereas it decreases with its generality (Fig. 4.2c). Together, body mass, trophic level and generality of the species initially extinct explain 97% of the variation in standardized robustness. The vulnerability of the species initially eliminated has no significant effect on robustness (Fig. 4.2d). The analyses of the data set without interferences yield similar results except for an additional significant, weak, negative effect of vulnerability on robustness (data not shown). Overall, our results suggest that extinctions of large-bodied species at low trophic levels of food webs with many prey species are most likely to cause secondary extinctions.

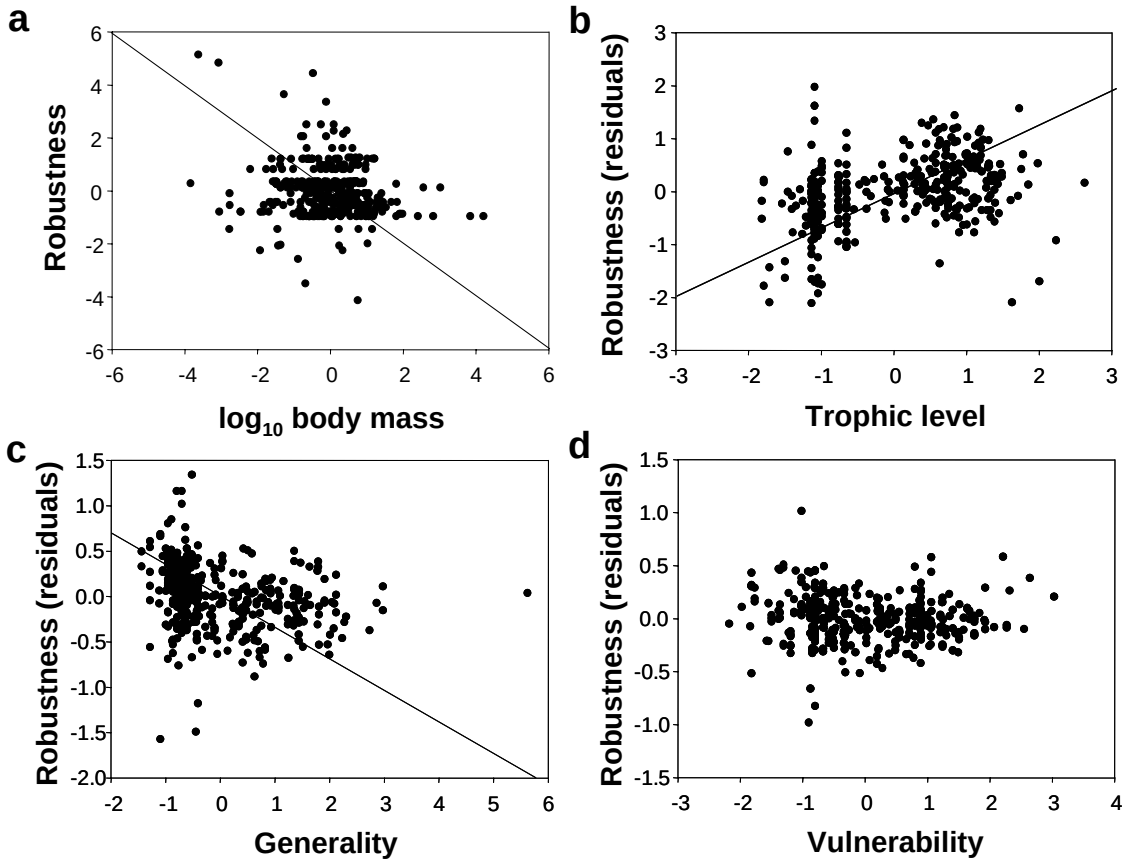


Figure 4.2 | Effects of characteristics of the species initially extinct on robustness. Stepwise RMA of standardized robustness depending on **(a)** $\log_{10}$*SE* body mass, correlation value *c* = -0.17, slope = -1 (lower 95% CL = -1.93, upper 95% CL = -0.52) intercept = -9.1 x 10^{-11}, R^2 = 0.59; **(b)** *SE* trophic level, *c* = 0.39, slope = 0.64 (0.51, 0.82), intercept = 2.59 x 10^{-10}, R^2 = 0.70; **(c)** *SE* generality, c = -0.26, slope = -0.35 (-0.52, -0.24), intercept = -5.00 x 10^{-11}, R^2 = 0.63; **(d)** *SE* vulnerability, (not significant, c = -0.09, slope = -0.22 (./. , ./.), intercept = 2.24 x 10^{-11}, R^2 = 0.55). Data and analyses based on simulations with predator interference. Note: Robustness of (b)-(e) represents residuals of prior analyses (see Methods regarding stepwise RMAs).

4.5 Discussion

Our analyses explore food-web robustness against species loss in dynamic models of large complex natural food webs. This approach goes beyond well-known limitations of both dynamic models of small food-web modules (Pimm 1979, 1980, Borrvall *et al.* 2000, Ebenman *et al.* 2004, Thébault *et al.* 2007) and structural models of complex food webs that lack dynamics (Solé & Montoya 2001, Dunne *et al.* 2002). At the food-web level, we found that robustness decreases with species diversity and increases with the number of basal species. Interestingly, these relationships are found in data sets with and without predator interference. The decrease of robustness with diversity

thus corroborates negative relationships between stability and diversity found in early linear stability analyses (May 1972, Pimm 1979, 1980) including analyses of small modules without intraspecific competition (Pimm *et al.* 1988). However, it contradicts positive diversity-robustness relationships found in interaction modules of functional groups with intraspecific competition (Borrvall *et al.* 2000, Ebenman *et al.* 2004). This contrasts recent findings that the presence or absence of intraspecific competition in food-web modules may be responsible for different robustness-diversity relationships (Thébault *et al.* 2007). Instead, we propose that increasing diversity within functional groups yields structural redundancy of species that provides an insurance against secondary extinctions (Borrvall *et al.* 2000, Ebenman *et al.* 2004, Thébault *et al.* 2007). In contrast, increasing diversity that is not directly related to structural redundancy destabilizes food-web dynamics as in prior model communities (May 1972, Pimm 1979, 1980) and the simulated empirical food webs of the present study.

We found only weak and inconclusive relationships between food-web robustness and connectance that were positive with interference competition or negative without interference. This may be explained by negative effects of connectance on interaction strengths in models with predator interference (Rall *et al.* 2008). Instead, we found a much stronger, positive effect of the number of basal species on robustness. This is consistently, as a higher number of basal species increases the overall bottom-up energy availability in food webs (i.e., more basal species provide more biomass at the basal level of the food web). Additionally, increasing diversity at the basal level increases the structural redundancy of multiple bottom-up energy pathways as in prior model studies (Borrvall *et al.* 2000, Ebenman *et al.* 2004, Thébault *et al.* 2007). This structural redundancy may account for robustness increases by providing insurance against secondary extinctions that may disrupt specific energy pathways.

At the species level, we find that primary extinctions of larger species are likely to trigger a stronger cascade of secondary extinctions than primary extinctions of smaller species. This is consistent with recent analyses, showing that high predator-prey body-mass ratios provide food-web stability (Emmerson & Raffaelli 2004, Brose *et al.* 2006b, Otto *et al.* 2007). Extinctions of large-bodied species reduce the average body-mass ratios of the food-webs, which may destabilize food-web dynamics and decrease food-web robustness. Corroborating other studies (Borrvall *et al.* 2000, Ebenman *et al.* 2004), we suggest that food-web robustness increases with the trophic level of the species initially removed. Extinctions at low trophic positions are more likely to cut off other species from their energy source at the base of the food web while loss of species at high trophic levels are less likely to cause such cascades of extinctions. We also find that robustness decreases with increasing generality of the species initially

extinct. Thus, the loss of a specialized predator is less likely to trigger a cascade of secondary extinctions than the loss of a generalist predator. The negative effect of generality on robustness in our dynamic simulations of natural food webs supports prior structural food-web studies suggesting that extinctions of highly connected species trigger more secondary extinctions than the loss of randomly chosen species that are on average less connected and less likely to cause other consumers to loose resources (Solé & Montoya 2001, Dunne *et al.* 2002). In general, extinctions of lowly connected species yields more localized effects that are not distributed across many other direct predator and prey species.

Our results suggest that global food-web parameters as well as individual species traits affect the risk of secondary extinctions after species loss. Our approach helps to overcome some limitations of prior studies such as the reduced complexity of food-web modules and the lack of dynamics in structural studies, but it also shares some of their simplifying assumptions. First, we ignore resource competition among basal species via their independent logistic growth and reduced competition among herbivores by maintaining basal species above a certain threshold. Parameterizing competition models for basal species (Brose *et al.* 2005) would require unavailable information regarding their nutrient uptake rates and is beyond the scope of this study. However, an important future direction of research involves including such interaction parameters at low trophic levels as they are known to have important implications for food-web robustness to loss of species such as keystone consumers (Brose *et al.* 2005). Second, the body-mass data of the food webs studied are subject to measurement errors (see Brose *et al.* 2006a for a detailed discussion) which lead us to use statistical analyses that are robust to such errors. Third, we assume a three-quarter power-law scaling of the biological rates with the species' body masses (Brown *et al.* 2004) even though the value of this exponent is actively debated (Makarieva *et al.* 2005, Meehan 2006, White *et al.* 2007). Still, additional simulations with different exponents suggest that our results appear qualitatively insensitive to variation within the range of debated values (data not shown). Fourth, each of the nine food webs studied comprises relatively few species (Table 4.1), which prevents corroborating our results based on pooled data with separate analyses of individual networks. Thus, our analyses identify broad trends across ecosystems rather than patterns within individual ecosystems.

Table 4.1 | Food webs studied.

Food web	*n*	C	No. basal	TL	omnivory	habitat	original publication	body-mass data
Benguela Bay	29	0.228	2	3.863	0.759	marine	(Yodzis 1998)	(Yodzis 1998)
Small Reef	50	0.222	3	3.630	0.860	marine	(Opitz 1996)	Riede (unpublished)
Carpinteria Salt Marsh	83	0.072	8	2.606	0.530	marine	(Lafferty *et al.* 2006)	Riede (unpublished)
Skipwith Pond	35	0.310	1	2.731	0.543	freshwater	(Warren 1989)	(Warren 1989)
Broadstone Stream	34	0.192	5	2.159	0.265	freshwater	(Woodward & Hildrew 2001)	(Woodward & Hildrew 2001)
Sierra Lakes	38	0.217	3	2.462	0.351	freshwater	(Harper-Smith *et al.* 2005)	(Harper-Smith *et al.* 2005)
Coachella Dessert	26	0.337	3	3.569	0.808	terrestrial	(Polis 1991)	Riede (unpublished)
Grand Cariçaie, clc2	116	0.073	15	2.596	0.422	terrestrial	(Cattin-Blandenier 2004)	(Cattin-Blandenier 2004)
Arizona Mountain Forest	33	0.063	5	2.338	0.212	terrestrial	(Cohen 1989)	Cohen 1989 and Riede (unpublished)

n = species richness, C = connectance, "No. basal" = number of basal species, TL = average of the prey-averaged trophic level of all species, omnivory = fraction of omnivores. Only predator-prey interactions, parasitic interactions are excluded.

Finally, we restrict our analyses to a small set of food-web and species attributes such as body mass and trophic level that can be quantified under a variety of field conditions. Additional network parameters that are less easily measured (see Brose *et al.* 2005) may explain more of the residual variation in food-web robustness against secondary extinctions. However, our focus on more empirically tractable parameters increases the chances that our predictions of the consequences of species loss in natural ecosystems may be more readily tested and applied.

4.6 Conclusions

Overall, our analyses suggest that the loss of large-bodied, generalist consumers at low trophic levels are much more likely to cause secondary extinctions than loss of small-bodied consumers at high trophic levels. Moreover, food webs of low diversity with a high number of basal species are most robust against secondary extinctions. This means, for example, that loss of large herbivores may disrupt ecosystems much more than loss of specialized top predators, especially in highly diverse ecosystems with relatively few plant species. Large consumers at low trophic levels provide a stable energy source for consumers at higher trophic levels, which stabilizes food chains (Otto *et al.* 2007). Critically, large species are particularly prone to extinction due to human induced changes in their environment (e.g., Petchey *et al.* 1999, Jackson *et al.* 2001, Duffy 2003, Petchey *et al.* 2004). While prior studies found that loss of large bodied species at high trophic levels may induce trophic cascades that alter the abundance of other species (Bascompte *et al.* 2005, Borer *et al.* 2005), our study suggests that loss of large bodied consumer species at low trophic levels such as large herbivores or plankton filter feeders may cause cascades that eliminate more species from the ecosystem. Ultimately, these effects may further propagate through food-web networks and lead to severe effects on ecosystem processes such as primary production. The potential for such effects make it a continuing research challenge to integrate knowledge of complex food-web structures (Dunne 2006), allometric population dynamics (Yodzis & Innes 1992) and risks of primary extinctions (Petchey *et al.* 2004) to produce a general framework for predicting the consequences of species loss in multitrophic systems on ecosystem functioning (Thébault *et al.* 2007).

4.7 References

Bascompte J., Melián C.J. & Salà E. (2005) Interaction strength combinations and the overfishing of a marine food web. *Proceedings Of The National Academy Of Sciences Of The United States Of America*, 102, 5443-5447

Beddington J.R. (1975) Mutual interference between parasites or predators and its effect on searching efficiency. *Journal of Animal Ecology*, 44, 331-340

Borer E.T., Seabloom E.W., Shurin J.B., Anderson K.E., Blanchette C.A., Broitman B., Cooper S.D. & Halpern B.S. (2005) What determines the strength of a trophic cascade? *Ecology*, 86, 528-537

Borrvall C., Ebenman B. & Jonsson T. (2000) Biodiversity lessens the risk of cascading extinction in model food webs. *Ecology Letters*, 3, 131-136

Brose U., Berlow E.L. & Martinez N.D. (2005) Scaling up keystone effects from simple to complex ecological networks. *Ecology Letters*, 8, 1317-1325

Brose U., Jonsson T., Berlow E.L., Warren P., Banašek-Richter C., Bersier L.F., Blanchard J.L., Brey T., Carpenter S.R., Cattin Blandenier M.-F., Cushing L., Dawah H.A., Dell T., Edwards F., Harper-Smith S., Jacob U., Ledger M.E., Martinez N.D., Memmott J., Mintenbeck K., Pinnegar J.K., Rall B.C., Rayner T., Reuman D.C., Ruess L., Ulrich W., Williams R.J., Woodward G. & Cohen J.E. (2006a) Consumer-resource body-size relationships in natural food webs. *Ecology*, 87, 2411-2417

Brose U., Williams R.J. & Martinez N.D. (2006b) Allometric scaling enhances stability in complex food webs. *Ecology Letters*, 9, 1228-1236

Brown J.H., Gillooly J.F., Allen A.P., Savage V.M. & West G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, 85, 1771-1789

Cattin-Blandenier M.-F. (2004) Food web ecology: models and application to conservation. PhD Thesis, *Institut de zoologie,* Université de Neuchâtel (Suisse)

Cohen J.E. (1989) Ecologists' Co-Operative Web Bank (ECOWeb), Version 1.0.0 Machine-readable data base of food webs. Rockefeller University, New York

De Angelis D.L., Goldstein R.A. & O'Neill R.V. (1975) A model for trophic interactions. *Ecology*, 56, 881-892

De Ruiter P.C., Wolters V., Moore J.C. & Winemiller K.O. (2005) Food web ecology: Playing Jenga and beyond. *Science*, 309, 68-70

Duffy J.E. (2003) Biodiversity loss, trophic skew and ecosystem functioning. *Ecology Letters*, 6, 680-687

Dunne J.A. (2006) The network structure of food webs. In: *Ecological networks: linking structure to dynamics in food webs* (eds. Pascual M & Dunne JA), pp. 27-86. Oxford University Press

Dunne J.A., Williams R.J. & Martinez M.D. (2002) Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters*, 5, 558-567

Ebenman B., Law R. & Borrvall C. (2004) Community viability analysis: The response of ecological communities to species loss. *Ecology*, 85, 2591-2600

Emmerson M.C. & Raffaelli D. (2004) Predator-prey body size, interaction strength and the stability of a real food web. *Journal of Animal Ecology*, 73, 399-409

Enquist B.J., West G.B., Charnov E.L. & Brown J.H. (1999) Allometric scaling of production and life-history variation in vascular plants. *Nature*, 401, 907-911

Harper-Smith S., Berlow E.L., Knapp R.A., Williams R.J. & Martinez N.D. (2005) Communicating ecology through food webs: Visualizing and quantifying the effects of stocking alpine lakes with fish. In: *Dynamic Food Webs: Multispecies assemblages, ecosystem development, and environmental change* (eds. De Ruiter P, Moore JC & Wolters V). Elsevier/Academic Press

Hughes J.B., Daily G.C. & Ehrlich P.R. (1997) Population diversity: its extent and extinction. *Science*, 278, 689-692

Jackson J.B.C., Kirby M.X., Berger W.H., Bjorndal K.A., Botsford L.W., Bourque B.J., Bradshaw R.H., Cooke R., Erlandson J., Estes J.A., Hughes T.P., Kidwell S., Lange C.B., Lenihan H.S., Pandolfi J.M., Peterson C.H., Steneck R.S., Tegner M.J. & Warner R.R. (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293, 629-638

Lafferty K.D., Dobson A.P. & Kuris A.M. (2006) Parasites dominate food web links. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 11211-11216

Loeuille N. & Loreau M. (2005) Evolutionary emergence of size-structured food webs. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 5761-5766

Luck G., Daily G.C. & Ehrlich P. (2003) Population diversity and ecosystem services. *Trends Ecol. Evol.*, 18, 331-336

Makarieva A.M., Gorshkov V.G. & Li B.L. (2005) Energetics of the smallest: do bacteria breathe at the same rate as whales? *Proceedings Of The Royal Society B-Biological Sciences*, 272, 2219-2224

May R.M. (1972) Will a large complex system be stable? *Nature*, 238, 413-414

Meehan T.D. (2006) Energy use and animal abundance in litter and soil communities. *Ecology*, 87, 1650-1658

Opitz S. (1996) *"Trophic interactions in caribbean coral reefs." Technical Report 43*. ICLARM, Manily.

Otto S.B., Rall B.C. & Brose U. (2007) Allometric degree distributions facilitate food-web stability. *Nature*, 450, 1226-1229

Paine R.T. (1966) Food web complexity and species diversity. *American Naturalist*, 100, 65-75

Petchey O.L., Downing A.L., Mittelbach G.G., Persson L., Steiner C.F., Warren P.H. & Woodward G. (2004) Species loss and the structure and functioning of multitrophic aquatic systems. *Oikos*, 104, 467-478

Petchey O.L., McPhearson P.T., Casey T.M. & Morin P.J. (1999) Environmental warming alters food-web structure and ecosystem function. *Nature*, 402, 69-72

Pimm S.L. (1979) Complexity And Stability - Another Look At Macarthur Original Hypothesis. *Oikos*, 33, 351-357

Pimm S.L. (1980) Food web design and the effect of species deletion. *Oikos*, 35, 139-149

Pimm S.L., Jones H.L. & Diamond J. (1988) On the risk of extinction. *American Naturalist*, 132, 757-785

Pimm S.L., Russell G.J., Gittleman J.L. & Brooks T.M. (1995) The Future of Biodiversity. *Science*, 269, 347-350

Polis G.A. (1991) Complex trophic interactions in deserts: an empirical critique of food-web theory. *American Naturalist*, 138, 123-155

Power M.E., Tilman D., Estes J., Menge B.A., Bond W.J., Mills L.S., Daily G., Castilla J.C., Lubchenco J. & Paine R.T. (1996) Challenges in the quest for keystones. *BioScience*, 46, 609-620

Rall B.C., Guill C. & Brose U. (2008) Food-web connectance and predator interference dampen the paradox of enrichment. *Oikos*, doi: 10.1111/j.2007.0030-1299.15491.x

Salà O.E., Chapin F.S., III, Armesto J.J., Berlow E., Bloomfield J., Dirzo R., Huber-Sanwald E., Huenneke L.F., Jackson R.B., Kinzig A., Leemans R., Lodge D.M., Mooney H.A., Oesterheld M., Poff N.L., Sykes M.T., Walker B.H., Walker M. & Wall D.H. (2000) Global biodiversity scenarios for the year 2100. *Science*, 287, 1771-1774

Solé R. & Montoya J.M. (2001) Complexity and fragility in ecological networks. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 1480, 2039-2045

Srinivasan U.T., Dunne J.A., Harte J. & Martinez N.D. (2007) Response of complex food webs to realistic extinction sequences. *Ecology*, 88, 671-682

Thébault E., Huber V. & Loreau M. (2007) Cascading extinctions and ecosystem functioning: contrasting effects of diversity depending on food web structure. *Oikos*, 116, 163-173

Warren P.H. (1989) Spatial and Temporal Variation in the Structure of a Fresh-Water Food Web. *Oikos*, 55, 299-311

White C.R., Cassey P. & Blackburn T.M. (2007) Allometric exponents do not support a universal metabolic allometry. *Ecology*, 88, 315-323

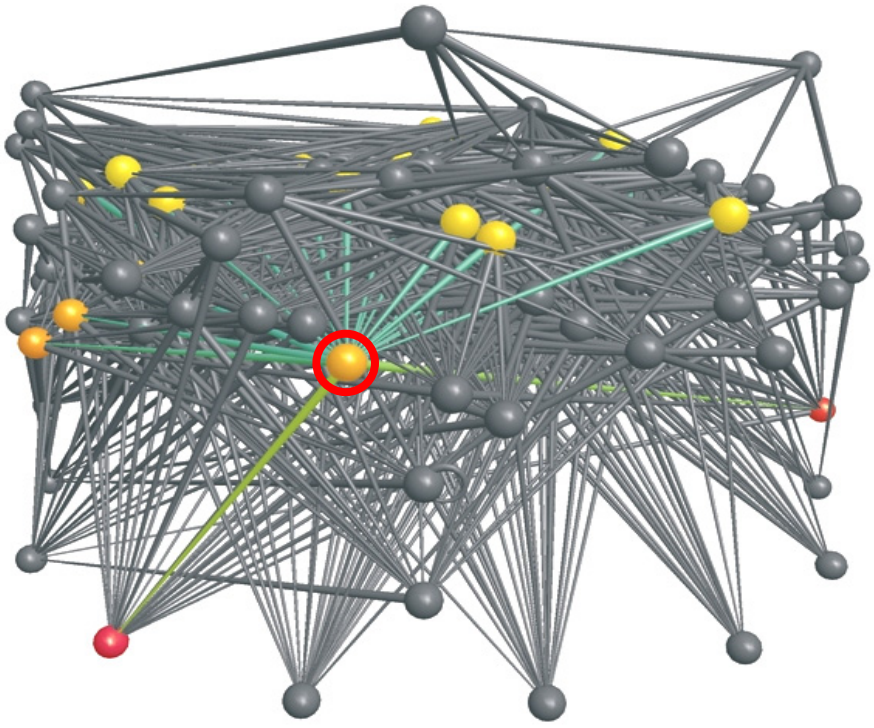
Woodward G. & Hildrew A.G. (2001) Invasion of a stream food web by a new top predator. *Journal of Animal Ecology*, 70, 273-288

Yodzis P. (1998) Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. *Journal of Animal Ecology*, 67, 635-658

Yodzis P. & Innes S. (1992) Body size and consumer-resource dynamics. *American Naturalist*, 139, 1151-1175

Chapter 5

Complexity, topology and diversity of food webs



Linkedness of one population in a complex food web. Pictured is a niche-model food web with a connectance of 0.18 and a diversity of 90 species. The encircled population is connected with 16 others of different trophic levels. The average link number per species and the link density, i.e., the connectance, are two important measures of bio-complexity in food webs.

Food web compiled with the help of www.foodwebs.org.

5.1 Abstract

Trophic scaling models describe how topological food-web properties such as the number of predator-prey links scale with community species richness. Early models predict that either the link density (i.e., the number of links per species) or the connectance (i.e., the linkage probability between any pair of species) is constant across communities. However, recent analyses suggest that both scaling models have to be rejected, and we discuss several hypotheses aiming to explain the scale-dependence of these complexity parameters. Based on recent food-web compilations, we further illustrate scale-dependence of food-web topology parameters. Our analyses also suggest significant power-law scaling relationships of the number of links, link density, connectance, the fractions of top and intermediate species, the standard deviations of generality and linkedness and the clustering coefficient with community species richness. Despite the lack of universal constants across the diversity scale, the scaling relationships between these properties and species richness indicate fundamental processes that determine food-web topology. Subsequently, we illustrate how recent models of food-web structure based on simple rule-based algorithms predict food-web topology. We conclude that these rules of niche-ordering, phylogenetic constraints and exponential degree distributions together with allometric constraints on predator-prey interactions represent promising cornerstones for future mechanistic models of food-web structure.

5.2 Introduction

Over the last several centuries, physicists have developed a variety of scaling laws such as Newton's law of universal gravitation holding that the gravitational force between two bodies is proportional to the product of their masses and the inverse square of their distance. Although the gravitational force varies along the distance scale, its behaviour is described by a scaling law, because the gravitational constant and the exponent (negative square) are constant with respect to distance. Scaling laws indicate, but do not prove, a fundamental process that governs the relationship between variables such as gravitational force and distance. In imitation of the grand laws of physics, ecologists have been searching for ecological scaling models that can be generalized across organisms, populations or ecosystems (Lange 2005, O'Hara 2005). Amongst the most prominent approaches, trophic scaling models predict relationships between topological food-web properties such as the number of predator-prey feeding interactions ('links') and the species richness of the community (Dunne 2006). In diversity-topology relationships, scale refers to the number of species, and

food-web ecologists have searched for universal food-web constants that equally apply to species-poor and species-rich ecosystems. Much of this trophic scaling debate has focused on parameters of food-web complexity such as the link density or connectance (Dunne 2006). More recent approaches were inspired by physicists' scaling laws and introduced scale-dependent properties but constant scaling exponents (Camacho *et al.* 2002a, Garlaschelli *et al.* 2003).

Here, we review concepts of trophic scaling models and test their predictions in worked examples using the most recent food-web data. We discuss potential explanations for the scale-dependence of complexity and review recent models of food-web topology.

5.3 Diversity-topology relationships

Early trophic scaling models suggested that link density – the number of links per species ($LD = L/S$) – is constant across food webs of varying species richness (Cohen & Briand 1984). This "link-species scaling law" is in agreement with the classical stability criterion of random networks holding that local population stability is maintained if link density falls below a critical threshold which in turn depends on the average interaction strength (May 1972). Subsequent early trophic scaling models proposed constancy of some food-web properties: the proportions of top species (T, species without consumers), intermediate species (I, species with consumers and resources) and basal species (B, species without resource species) (Briand & Cohen 1984), and constant proportions of T-I, T-B, I-I and I-B links (Cohen & Briand 1984). Empirical tests using early food-web data supported these scaling laws (Briand & Cohen 1984, Cohen & Briand 1984, Cohen *et al.* 1990), but the quality of the supporting food-web data has been questioned (Paine 1988, Polis 1991, Hall & Raffaelli 1993).

Following studies based on data of higher quality demonstrated that link density, the proportions of top, intermediate and basal species, and the proportions of T-I, T-B, I-I and I-B links are not constant across the diversity scale (Schoener 1989, Warren 1989, Winemiller 1990, Hall & Raffaelli 1991, Martinez 1991, 1993a). Earlier findings of scale-invariance were consequently ascribed to inadequate sampling effort, strong species aggregation and poor data resolution (Hall & Raffaelli 1991, Martinez 1991, 1993b, Goldwasser & Roughgarden 1997, Bersier *et al.* 1999, Martinez *et al.* 1999).

While the improved data demonstrated scale dependence of link density, an alternative hypothesis proposed connectance – the linkage probability of any pair of species in the food web ($C = L/S^2$) – to be constant across ecosystems of variable

species richness (Martinez 1992). While models with constant link density assume that any species can consume a fixed number of the coexisting species, the constant-connectance model holds that any species can consume a fixed fraction of the coexisting species. Initially, as the quality of the food-web data used improved the constant-connectance hypothesis found support (Martinez 1992, 1993a, Spencer & Warren 1996). Analyses of more recent food-web data, however, suggest that neither link density nor connectance are constant across the diversity scale (Schmid-Araya *et al.* 2002, Montoya & Solé 2003, Brose *et al.* 2004, Dunne 2006).

5.4 Worked example: Diversity-complexity relationships

We illustrate trophic scaling theories using a data set of 23 food webs from a variety of habitats (see Table 5.1 for an overview of the food webs). This compilation includes 17 food webs that have been used in prior meta-studies (Williams & Martinez 2000, Montoya & Solé 2003, Cattin *et al.* 2004, Dunne *et al.* 2004, Stouffer *et al.* 2005, Dunne 2006) while adding six food webs from a recent meta-study on natural consumer-resource body-mass ratios (Brose *et al.* 2006). To avoid pseudo-replication we have used only one of the food webs from studies with multiple sites (Havens 1992, Townsend *et al.* 1998, Cattin-Blandenier 2004). Additionally, we have excluded those food webs that are dominated by parasitoid or parasitic interactions. This choice does not imply that these interactions are not of importance for the structure and function of the food webs, but they are governed by other physical constraints than predator-prey interactions (Brose *et al.* 2006), which results in different complexity patterns (Lafferty *et al.* 2006). Maintaining a focus on predator-prey interactions thus helps elucidate the underlying processes. The data compilation analyzed here includes food webs from five terrestrial sites, seven lakes or ponds, three streams, four brack-waters and four marine sites (Table 5.1).

Table 5.1. | Structural characteristics of 23 food webs.

	Taxa	S	C	L/S	L	TL	T	I	B	Reference
Terrestrial										
Coachella Valley	30	29	0.31	9.0	262	3.89	0	90	10	(Polis 1991)
St. Martin Island	44	42	0.12	4.9	205	2.61	17	69	14	(Goldwasser & Roughgarden 1993)
Broom Source Web	154	85	0.03	2.6	223	3.07	59	40	1	(Memmott *et al.* 2000)
Grand Cariçaie – Scc2	152	134	0.07	9.2	1235	2.60	2	86	12	(Cattin-Blandenier 2004)
El Verde	156	155	0.06	9.7	1509	2.94	13	69	18	(Waide & Reagan 1996)
Lake / Pond										
Sierra Lakes	37	19	0.25	19	0.25	19	0.25	19	0.25	(Harper-Smith *et al.* 2005)
Tuesday Lake 1984	50	21	0.16	21	0.16	21	0.16	21	0.16	(Jonsson *et al.* 2005)
Skipwith Pond	35	25	0.32	25	0.32	25	0.32	25	0.32	(Warren 1989)
Bridge Brook Lake	75	25	0.17	25	0.17	25	0.17	25	0.17	(Havens 1992)
Little Rock Lake	181	92	0.12	92	0.12	92	0.12	92	0.12	(Martinez 1991)
Mirror Lake	586	156	0.14	156	0.14	156	0.14	156	0.14	
Lake Tahoe	800	172	0.13	172	0.13	172	0.13	172	0.13	
Stream										
Broadstone Stream	34	30	0.21	30	0.21	30	0.21	30	0.21	(Woodward *et al.* 2005)
Canton Creek	108	102	0.07	102	0.07	102	0.07	102	0.07	(Townsend *et al.* 1998)
Stony Stream	112	109	0.07	109	0.07	109	0.07	109	0.07	(Townsend *et al.* 1998)
Estuary / Salt Marsh										
Chesapeake Bay	33	31	0.07	31	0.07	31	0.07	31	0.07	(Baird & Ulanowicz 1989)
St. Mark's Estuary	48	48	0.10	48	0.10	48	0.10	48	0.10	(Christian & Luczkovich 1999)
Carpenteria*	83	74	0.08	74	0.08	74	0.08	74	0.08	(Lafferty *et al.* 2006)
Ythan Estuary*	92	83	0.06	83	0.06	83	0.06	83	0.06	(Hall & Raffaelli 1991)
Marine										
Benguela System	29	29	0.24	29	0.24	29	0.24	29	0.24	(Yodzis 1998)
Carribean Reef, small	50	50	0.22	50	0.22	50	0.22	50	0.22	(Opitz 1996)
NE US Shelf	81	79	0.22	79	0.22	79	0.22	79	0.22	(Link 2002)
Weddell Sea	492	290	0.09	290	0.09	290	0.09	290	0.09	(Ute Jacob, unpublished)

Taxa = number of taxonomic species; all subsequent characteristics are calculated for the trophic food webs: S = species richness, C = connectance, L/S = links per species, L = links, TL = mean prey-averaged trophic level, T = top species richness, I = intermediate species richness, B = basal species richness. * Food web versions without parasites.

The number of taxonomic species ranges between 29 and 800, and the trophic food-webs include 19 to 290 trophic species. 16 food-web properties were calculated for each of the 23 trophic food webs studied (see Fig. 5.1 and 5.2 for an overview). We analyzed the relationships between these food-web properties and diversity (i.e., species richness) by fitting non-linear power-law regression models. We tested for significant deviations of the power-law exponents, $x \pm \sigma$ (mean ± s.m.e.), from a null hypothesis, μ, by calculating the normally distributed probabilities of the z-scores:

$$p\left(z = \frac{x - \mu}{\sigma} \right) .$$

Significant deviation from zero (μ = 0) indicate scale-dependence of the food-web property.

First, we illustrate the scaling of link richness, link density (links per species) and connectance with diversity (Fig. 5.1). When the number of trophic links (L) of food webs is plotted against species richness (S) the "constant-connectance" hypothesis predicts a power-law exponent of two, μ = 2, while the link-species scaling law predicts an exponent of one, μ = 1 (Martinez 1992). In our data, we found an exponent of 1.83 ± 0.14 (mean ± s.m.e., Fig. 5.1a), which does not differ from two ($p = 0.215$), but deviates significantly from one ($p < 0.001$). Exclusion of the most diverse food web (Weddell Sea) from this analysis does not modify the result. Additional analyses showed that link density increased significantly with diversity (Fig. 5.1b, $p < 0.001$), whereas connectance decreased significantly with diversity (Fig. 5.1c, $p < 0.001$). Thus, despite a link-species scaling not significantly different from two (Fig. 5.1a) our analyses suggest that both scaling models, the link-species scaling law and the constant-connectance hypothesis, have to be rejected (Fig. 5.1b, c). This indicates that more diverse webs are characterized by a high number of links per species but low connectance. Thus, our analyses support a recent change in paradigm from constant to scale-dependent connectance (Schmid-Araya *et al.* 2002, Montoya & Solé 2003, Brose *et al.* 2004, Dunne 2006).

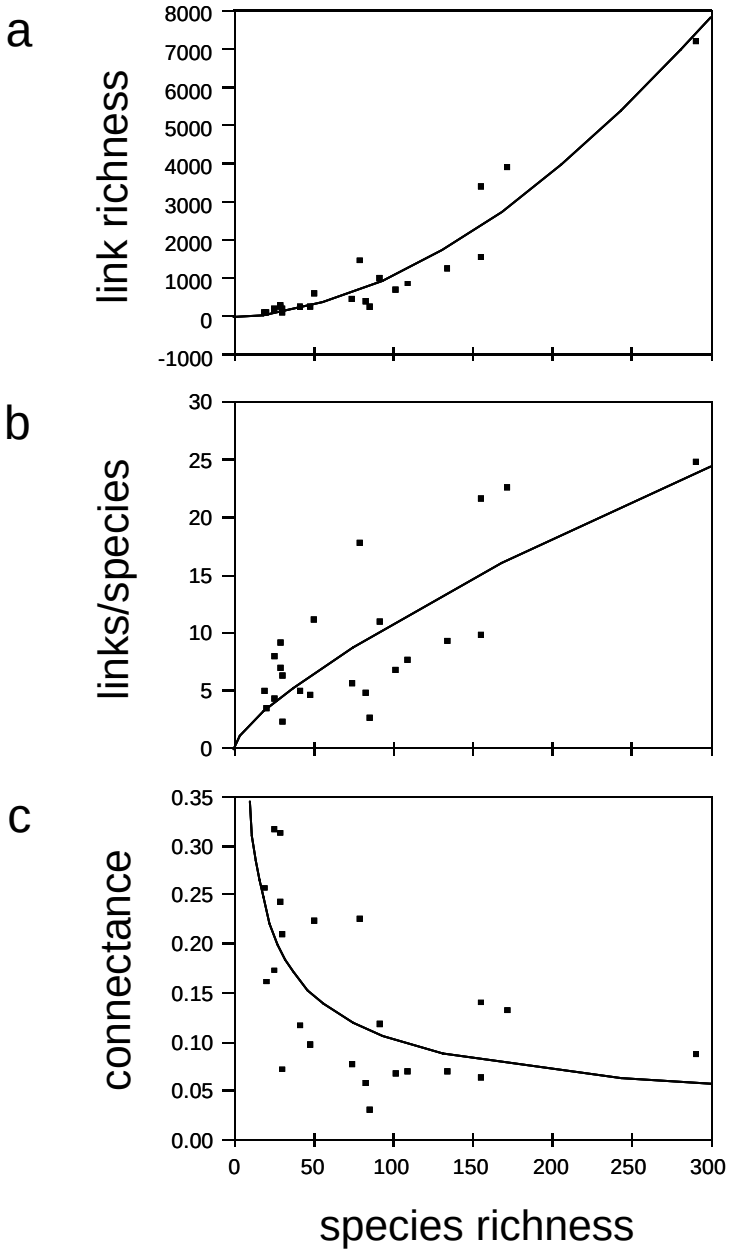


Figure 5.1 | Diversity-complexity relationships. Scaling of **(a)** trophic link richness (exponent = 1.83 ± 0.14, constant = 0.23 ± 0.17, R^2 = 0.93); **(b)** links per species (exponent = 0.73 ± 0.14, constant = 0.37 ± 0.26, R^2 = 0.57) and **(c)** connectance with species richness (exponent = - 0.53 ± 0.15, constant = 1.18 ± 0.64, R^2 = 0.43).

5.5 Explanations for the scale-dependence of complexity

Several potential explanations for the scale-dependence of links per species and connectance can be identified. First, in communities with many interacting species, the decrease of connectance with diversity may result from a methodological artefact (Paine 1988), namely that the difficulty of identifying trophic links among a large number of species increases with species richness. This yields a potentially lower sampling intensity of links in more diverse food webs, which would account for a decrease in connectance with species richness (Goldwasser & Roughgarden 1997, Bersier *et al.* 1999, Martinez *et al.* 1999). Ultimately, an adequate sampling effort can only be guaranteed if yield-effort curves demonstrate saturation in link richness with sampling effort for every food web (Woodward & Hildrew 2001) or if extrapolation methods suggest a high sampling coverage (Brose *et al.* 2003, Brose & Martinez 2004). While this is certainly desirable for future food-web compilations, the currently available data is lacking this information and we cannot entirely rule out that the sampling effect contributes to the decrease in connectance with species richness.

Second, the increase in links per species with species richness could be primarily driven by an increasing number of weak links (i.e., links with a low energy flux), whereas the number of strong links per species might be constant. Empirical studies have indeed found interaction strengths to be highly skewed towards many weak and a few strong links (Paine 1992, Goldwasser & Roughgarden 1993, Fagan & Hurd 1994, Wootton 1997). Taking the variability in energy flux between links into consideration, initial tests found that the overall number of links per species increases with species richness, whereas quantitative versions of link density weighing the links according to their energy flux remain scale invariant (Banašek-Richter *et al.* 2005). Thus, the distribution of energy fluxes becomes more unequal as systems accrue in species number, possibly due to the increase in weak links. This implies that species can have strong interactions with only a fixed number of the coexisting species, while the number of weak interactions continuously increases with species richness. While the former "sampling effect" suggests that the number of sampled links is too low in more diverse food webs, the approach of using quantitative food-web data along with their corresponding descriptors (Bersier *et al.* 2002, Banašek-Richter *et al.* 2004) implies that most of the links in diverse food webs are weak and may even be unimportant for calculating connectance or link density. However, this implication needs to be reconciled with recent theoretical work stressing the importance of weak links for the organisation of natural food webs (McCann *et al.* 1998, Berlow 1999, Navarrete & Berlow 2006).

Third, food-web stability might require that during community assembly diversity is negatively correlated to complexity. This argument is based on the finding that species-poor communities exhibit Poissonian degree distributions (i.e., the frequency of species with links), whereas species-rich communities have more skewed distributions (Montoya & Solé 2003). Thus, increasing diversity primarily leads to an increase in species with few links, which decreases connectance. Classic stability analyses have shown that population stability decreases with both, diversity and connectance (May 1972). When natural food webs assemble, the destabilizing effect of increasing diversity needs to be balanced by a resulting decrease in connectance to avoid instability (Montoya & Solé 2003). This stability argument mechanistically links variation in species diversity and community complexity.

Fourth, processes that increase diversity may reduce species' co-existence, which decreases connectance. However, the constant-connectance and link-species scaling models assume that species may consume a fix fraction or a fix number, respectively, of the co-existing species (Cohen & Briand 1984, Martinez 1992). Thus, these models predict constancy in the scaling exponents only if co-existence does not change with diversity. However, potential consumer and resource species do not necessarily co-exist in meta-communities at larger spatial scales (Brose *et al.* 2004). If species richness across food webs increases with the spatial extent of the habitats, connectance will decrease with species richness due to a decrease in predator-prey co-occurrence. Link-area models based on this argument have successfully predicted the number of links, links density and connectance of aquatic food webs ranging in spatial scale from local habitats to landscapes (Brose *et al.* 2004). Interestingly, the exponent of the power-law link-species model at the scale of local habitats was close to two as predicted by the constant-connectance model, whereas it decreases to lower values when larger spatial scales are included and where species' co-existence may break down (Brose *et al.* 2004). Similarly, predator-prey co-existence may also collapse with increasing habitat complexity (Keitt 1997). Increasing habitat complexity or architectural complexity of the vegetation leads to higher species richness as many predators are specialized on specific sub-habitats such as distinct vegetation layers (Brose 2003, Tews *et al.* 2004). The localized occurrence of these predators in sub-habitats may yield reduced connectance as the predators do not co-exist with all prey species that fall within their feeding niche. Interestingly, strong support for the constant-connectance hypothesis comes from the pelagic food webs of 50 lakes (Martinez 1993a) and aquatic microcosms (Spencer & Warren 1996). In these very homogenous habitats, increases in habitat complexity play no role in increasing species richness – a constellation which sets the frame for constant connectance. In contrast, increasing species richness in stream communities was correlated with decreases in

connectance, which may be explained by variation in habitat complexity (Schmid-Araya *et al.* 2002).

Fifth, predator specialisation may decrease connectance in more diverse food webs. The feeding ranges of consumers may be limited to specific body-size ranges of potential resource species. If the body-size range increases with the species richness of the community, connectance will decrease with community diversity due to physical feeding constraints. Moreover, the possibility to decide upon multiple prey species increases for any predator with increasing species richness. Therefore, predators in more diverse communities may specialize on a subset of their potential feeding niche that includes prey species that are easier to exploit or less defended. Additionally, uneven abundances of potential prey within the feeding range may induce a predator switching behaviour that creates temporally unexploited prey of low abundances. This hypothesis suggests that the prey abundance of the unrealized links should be lower than the prey abundance of the realized links. In compliance with these arguments, Beckerman *et al.* (2006) offer a mechanistic explanation for connectance. Based on optimal foraging theory, they assume that predators preferentially feed on the energetically most rewarding prey. Their "diet breadth model" relates food-web complexity to species' foraging biology and does well in predicting the scaling of connectance with species richness (Beckerman *et al.* 2006). The optimization constraints regarding the species' foraging behaviour thus entail the complexity of their food web.

Each of the aforementioned hypotheses may be partial in explaining the variance of connectance with species richness, and they are not mutually exclusive. Most likely, the mechanisms underlying the observed patterns are multi-causal and vary with the spatial scale. The "sampling hypothesis" suggests that mere sampling artefacts are responsible for the decrease in connectance with species richness, whereas all other hypotheses presume ecological processes behind this pattern. In addition to the empirical pattern (Fig. 5.1), these biological hypotheses substantiate the conclusion that connectance is not constant but decreases with diversity. This supports a change in paradigm from constant to scale-dependent connectance in community food webs.

5.6 *Worked example: diversity-topology relationships*

Supplementary to reviewing and discussing the common perception of scale-dependency of link density and connectance, we analyzed the scaling of 13 additional food-web properties with diversity (Fig. 5.2). We found that the proportions of intermediate and top species and the standard deviations of linkedness and generality increased significantly with species richness, whereas the clustering coefficient decreased significantly. Moreover, our data suggest almost significant increases in the proportion of carnivores ($p = 0.067$) and the maximum trophic level of the food webs ($p = 0.075$). The increases in the maximum trophic levels of the food webs with diversity may be a consequence of an increasing proportion of top species. We anticipate that additional food-web data to be collected will support these trends. The exponents of the other power-law trophic scaling relationships did not differ significantly from zero (Fig. 5.2).

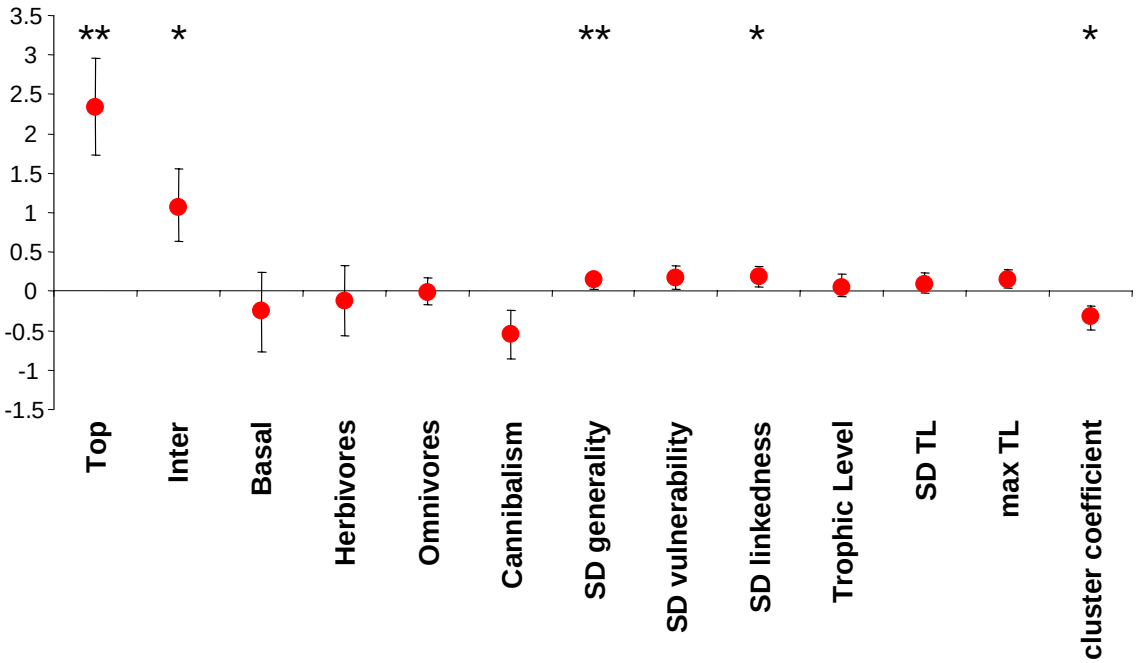


Figure 5.2 | Exponents (mean ± s.m.e.) of the power-law diversity-topology relationships. Proportions of Top, intermediate (Inter), Basal species, Herbivores, Omnivores and cannibals (Cannibalism); standard deviations (SD) of generality, vulnerability and linkedness; the mean prey averaged Trophic Level and its standard deviation (SD TL) and maximum (max TL); and the cluster coefficient. Stars indicate significant deviations of the exponents from zero: ** = $p < 0.01$, * = $p < 0.05$.

Species-rich food webs thus have a higher proportion of intermediate and top species, which should result in a lower proportion of basal species, but this trend – though negative – was not significant. Interestingly, our results corroborate the conclusion of prior studies that the fraction of intermediate species increases with diversity, whereas they oppose their finding that the fractions of top and basal species decrease (Schoener 1989, Warren 1989, Winemiller 1990, Hall & Raffaelli 1991, Martinez 1991, 1993a). This suggests that species-rich food webs might have more top and basal species than previously anticipated. This may partially be explained by the low resolution of basal species in some prior data sets.

Our analyses also suggest that species-rich food webs exhibit a higher variability in the generality (i.e., the number of predator links) and linkedness (i.e., the overall number of links) of the species. Consistent with a prior study (Montoya & Solé 2003), this suggests that species-rich food webs have a more uneven distribution of links amongst the species, which may increase population stability. Moreover, we found that the clustering coefficient (i.e., the likelihood that two species that are linked to the same species are also linked to each other) is inversely proportional to diversity, which corroborates prior analytical results based on niche-model food webs (Camacho *et al.* 2002b). Together with the analytical finding that the mean shortest path length between species decreases with diversity (Williams *et al.* 2002), this suggests that species-rich food webs are less compartmentalized than species-poor food webs.

In our analyses, seven food-web properties did not exhibit a significant power-law scaling with diversity: the proportions of basal species, herbivores and omnivores, the standard deviation of vulnerability, and the mean, maximum and standard deviation of the trophic level (Fig. 5.2). While this might be interpreted that these food-web properties are scale independent, their high coefficients of variation (ranging from 29% to 168 %) imply that they are not constant. Together, our results and those of prior studies (Schmid-Araya *et al.* 2002, Montoya & Solé 2003, Brose *et al.* 2004, Dunne 2006) suggest that food webs do not exhibit scale-independent constants. However, consistent with other recent work on trophic scaling laws (Camacho *et al.* 2002a, Garlaschelli *et al.* 2003), these findings also suggest that many scale-dependent food-web properties follow diversity-topology relationships with constant scaling exponents.

5.7 Models of food-web topology

Food-web topology is tightly related to species richness (*S*) and the connectance (*C*) of a food web. This becomes apparent in simple, stochastic models that use these two properties as their only input parameters and successfully predict a variety of network structure properties of empirical food webs (Cohen *et al.* 1990, Williams & Martinez 2000, Cattin *et al.* 2004, Dunne *et al.* 2004, Stouffer *et al.* 2005). These stochastic models share the same three-step setup: (1) *S* and *C* are set to the values of a particular empirical food web of interest, (2) species are randomly distributed on a single niche axis (i.e., random assignment of a "niche value" between 0 to 1), and (3) feeding links, whose number is determined by the empirical value of *C*, are distributed among the species. The models differ with regard to how feeding links are distributed. In the cascade model (Cohen *et al.* 1990), as modified to fit the format described above (Williams & Martinez 2000), each species has a fixed probability of consuming species with niche values less than its own. This establishes a feeding hierarchy and disallows cannibalism and feeding loops (i.e., species *a* feeds on species *b* feeds on species *c* feeds on species *a*). In the niche model (Williams & Martinez 2000, Camacho *et al.* 2002a, Dunne *et al.* 2004), a species consumes all species that fall within a feeding range whose randomly assigned centre is equal to or lower than the niche value of the consumer, and whose randomly assigned breadth is drawn from a β-distributed probability density function. This link distribution scheme allows for cannibalism and looping and introduces contiguity (intervality) of feeding. Assigning links according to the nested hierarchy model (Cattin *et al.* 2004), is a multi-stage process: a link is randomly drawn between consumer species *i* and prey species *j*, the later having a lower niche value than the former. If *j* is also fed on by other species, the next link is assigned randomly to one of the species consumed by the set of species that share at least one prey species, one of them being species *j*. If more links are required, they are randomly assigned to species without predators and with lower niche values, and as a last resort to species with greater niche values. These rules, which are also constrained by a β-distribution, attempt to incorporate phylogenetic and adaptive constraints into how feeding links are assigned, and relax the intervality assumption of the niche model. In the generalized cascade model (Stouffer *et al.* 2005) each species has a specific probability of consuming species with lower niche values, which is drawn from an approximately exponential distribution. This model resembles the cascade model, but relies on a degree distribution similar to the β-distribution of the niche and nested hierarchy models.

Recent evaluations compared how successfully these models predict food-web properties such as the fraction of top, intermediate and basal species or the average

trophic level of the food web (Williams & Martinez 2000, Cattin *et al.* 2004, Dunne *et al.* 2004, Stouffer *et al.* 2005). These evaluations create a set of model webs (usually 1000) for each type of model with S and C of an empirical food web. Subsequently, the difference between the model mean for a property and its empirical counterpart is used for the evaluation. Several evaluations have indicated a similar fit of the niche, nested-hierarchy and generalized-cascade models and an order of magnitude improvement in their fit over the cascade model (Williams & Martinez 2000, Cattin *et al.* 2004, Dunne *et al.* 2004, Stouffer *et al.* 2005). Surprisingly, the overall success of the recent models (i.e., the niche, nested-hierarchy and the generalized-cascade model) is governed by only two conditions: (1) the species are ranked on a single niche axis, and (2) each species has an exponentially decaying probability of feeding on lower-ranked species (Stouffer *et al.* 2005). Other conditions such as feeding contiguity and the possibility of eating at higher niche values are relevant in the more fine-grained ways that these models differ in how they predict food-web structure. For instance, the niche model assumes contiguous feeding ranges (i.e., all species within the feeding range are consumed), whereas the nested-hierarchy and the generalized-cascade model create interval feeding niches (i.e., gaps within the feeding ranges indicate species that are not consumed). Interestingly, a recent analysis of empirical food webs has demonstrated that while gaps in the feeding niches of consumers occur, the removal from contiguous feeding ranges is not significant (Stouffer *et al.* 2006).

5.8 Conclusions

Consistent with previous studies (Schmid-Araya *et al.* 2002, Montoya & Solé 2003, Brose *et al.* 2004, Dunne 2006), our results suggest that neither links per species nor connectance are scale-invariant constants. After several decades of debate in the trophic scaling theory it remains thus unlikely that there are universal scale-independent constants in natural food webs that hold from communities that are low in diversity to those that are species rich. Nevertheless, recent work supports trophic scaling models predicting relationships between parameters of food-web topology and diversity with constant scaling exponents (Camacho *et al.* 2002a, Garlaschelli *et al.* 2003). While these scaling relationships are certainly not as simple as often desired, they enable an understanding of the interrelation of the many parameters of complex food webs. A mechanistic understanding of why complex food webs appear to share a fundamental network structure mediated by species richness and connectance is yet to be gained – just as physicists are still lacking a mechanistic explanation of the gravitational force several centuries after Newton phrased the universal law of gravitation.

Nevertheless, theoretical aspects of food-web ecology have made substantial progress in the last decade. Recent structural food-web models (Williams & Martinez 2000, Cattin *et al.* 2004, Stouffer *et al.* 2005) implement dependence of network topology on species richness and connectance and predict food-web properties depending on contiguous feeding ranges within an ordered set of species' niches (Williams & Martinez 2000), phylogenetic constraints on feeding interactions (Cattin *et al.* 2004) and exponential degree distributions (Stouffer *et al.* 2005). The integration of such research with core concepts from other research areas, such as the body-size constraints on predator-prey interactions (Wootton & Emmerson 2005, Beckerman *et al.* 2006, Brose *et al.* 2006), is a very promising way to start to develop a mechanistic basis for observed trophic patterns.

5.9 References

Baird D. & Ulanowicz R.E. (1989) The Seasonal Dynamics Of The Chesapeake Bay Ecosystem. *Ecological Monographs*, 59, 329-364

Banašek-Richter C., Cattin-Blandenier M.-F. & Bersier L.-F. (2005) Food web structure: from scale invariance to scale dependence, and back again? In: *Dynamic food webs* (eds. De Ruiter PC, Wolters V & Moore JC), pp. 48-55. Academic Press, Burlington, USA

Banašek-Richter C., Cattin M.F. & Bersier L.F. (2004) Sampling effects and the robustness of quantitative and qualitative food-web descriptors. *Journal of Theoretical Biology*, 226, 23-32

Beckerman A.P., Petchey O.L. & Warren P.H. (2006) Foraging biology predicts food web complexity. *Proceedings of the National Academy of Sciences USA*, 103, 13745-13749

Berlow E.L. (1999) Strong effects of weak interactions in ecological communities. *Nature*, 398, 330-334

Bersier L.F., Banašek-Richter C. & Cattin M.F. (2002) Quantitative descriptors of food-web matrices. *Ecology*, 83, 2394-2407

Bersier L.F., Dixon P. & Sugihara G. (1999) Scale-invariant or scale-dependent behavior of the link density property in food webs: a matter of sampling effort? *American Naturalist*, 153, 676-682

Briand F. & Cohen J.E. (1984) Community Food Webs Have Scale-Invariant Structure. *Nature*, 307, 264-267

Brose U. (2003) Bottom-up control of carabid beetle communities in early successional wetlands: mediated by vegetation structure or plant diversity? *Oecologia*, 135, 407-413

Brose U., Jonsson T., Berlow E.L., Warren P., Banašek-Richter C., Bersier L.F., Blanchard J.L., Brey T., Carpenter S.R., Cattin-Blandenier M.-F., Cushing L., Dawah H.A., Dell T., Edwards F., Harper-Smith S., Jacob U., Ledger M.E., Martinez N.D., Memmott J., Mintenbeck K., Pinnegar J.K., Rall B.C., Rayner T., Reuman D.C., Ruess L., Ulrich W., Williams R.J., Woodward G. & Cohen J.E. (2006) Consumer-resource body-size relationships in natural food webs. *Ecology*, 87, 2411-2417

Brose U. & Martinez N.D. (2004) Estimating the richness of species with variable mobility. *Oikos*, 105, 292-300

Brose U., Martinez N.D. & Williams R.J. (2003) Estimating species richness: Sensitivity to sample coverage and insensitivity to spatial patterns. *Ecology*, 84, 2364-2377

Brose U., Ostling A., Harrison K. & Martinez N.D. (2004) Unified spatial scaling of species and their trophic interactions. *Nature*, 428, 167-171

Camacho J., Guimera R. & Amaral L.A.N. (2002a) Analytical solution of a model for complex food webs. *Physical Review E*, 65, 030901

Camacho J., Guimera R. & Amaral L.A.N. (2002b) Robust patterns in food web structure. *Physical Review Letters*, 88, 228102

Cattin-Blandenier M.-F. (2004) Food-web ecology: models and application to conservation. PhD Thesis, *Institut de zoologie,* Université de Neuchâtel (Suisse)

Cattin M.F., Bersier L.F., Banašek-Richter C., Baltensperger R. & Gabriel J.P. (2004) Phylogenetic constraints and adaptation explain food-web structure. *Nature*, 427, 835-839

Christian R.R. & Luczkovich J.J. (1999) Organizing and understanding a winter's seagrass food web network through effective trophic levels. *Ecological Modelling*, 117, 99-124

Cohen J.E., Briand E.F. & Newman C.M. (1990) *Community Food Webs: Data and Theory*. Springer-Verlag, New York.

Cohen J.E. & Briand F. (1984) Trophic Links Of Community Food Webs. *Proceedings Of The National Academy Of Sciences Of The United States Of America-Biological Sciences*, 81, 4105-4109

Dunne J.A. (2006) The network structure of food webs. In: *Ecological networks: linking structure to dynamics in food webs* (eds. Pascual M & Dunne JA), pp. 27-86. Oxford University Press

Dunne J.A., Williams R.J. & Martinez N.D. (2004) Network structure and robustness of marine food webs. *Marine Ecology-Progress Series*, 273, 291-302

Fagan W.F. & Hurd L.E. (1994) Hatch density variation of a generalist arthropod predator: population consequences and community impact. *Ecology*, 75, 2022-2032

Garlaschelli D., Caldarelli G. & Pietronero L. (2003) Universal scaling relations in food webs. *Nature*, 423, 165-168

Goldwasser L. & Roughgarden J. (1993) Construction And Analysis Of A Large Caribbean Food Web. *Ecology*, 74, 1216-1233

Goldwasser L. & Roughgarden J. (1997) Sampling effects and the estimation of food-web properties. *Ecology*, 78, 41-54

Hall S.J. & Raffaelli D. (1991) Food-Web Patterns - Lessons From A Species-Rich Web. *Journal Of Animal Ecology*, 60, 823-842

Hall S.J. & Raffaelli D.G. (1993) Food webs: theory and reality. In: *Advances in Ecological Research* (eds. Begon M & Fitter AH), pp. 187-239. Academic Press, London

Harper-Smith S., Berlow E.L., Knapp R.A., Williams R.J. & Martinez N.D. (2005) Communicating ecology through food webs: Visualizing and quantifying the effects of stocking alpine lakes with fish. In: *Dynamic Food Webs: Multispecies assemblages,*

ecosystem development, and environmental change (eds. De Ruiter P, Moore JC & Wolters V). Elsevier/Academic Press

Havens K. (1992) Scale And Structure In Natural Food Webs. *Science*, 257, 1107-1109

Jonsson T., Cohen J.E. & Carpenter S.R. (2005) Food webs, body size, and species abundance in ecological community description. *Advances in Ecological Research*, 36, 1-84

Keitt T.H. (1997) Stability and complexity on a lattice: coexistence of species in an individual-based food web model. *Ecological Modelling*, 102, 243-258

Lafferty K.D., Dobson A.P. & Kuris A.M. (2006) Parasites dominate food web links. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 11211-11216

Lange M. (2005) Ecological laws: what would they be and why would they matter? *Oikos*, 110, 394-403

Link J. (2002) Does food web theory work for marine ecosystems. *Marine Ecology Progress Series*, 230, 1-9

Martinez N.D. (1991) Artifacts Or Attributes - Effects Of Resolution On The Little-Rock Lake Food Web. *Ecological Monographs*, 61, 367-392

Martinez N.D. (1992) Constant connectance in community food webs. *American Naturalist*, 139, 1208-1218

Martinez N.D. (1993a) Effects of scale on food web structure. *Science*, 260, 242-243

Martinez N.D. (1993b) Effects of resolution on food web structure. *Oikos*, 66, 403-412

Martinez N.D., Hawkins B.A., Dawah H.A. & Feifarek B.P. (1999) Effects of sampling effort on characterization of food-web structure. *Ecology*, 80, 1044-1055

May R.M. (1972) Will a large complex system be stable? *Nature*, 238, 413-414

McCann K., Hastings A. & Huxel G.R. (1998) Weak trophic interactions and the balance of nature. *Nature*, 395, 794-798

Memmott J., Martinez N.D. & Cohen J.E. (2000) Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web. *Journal of Animal Ecology*, 69, 1-15

Montoya J.M. & Solé R.V. (2003) Topological properties of food webs: from real data to community assembly models. *Oikos*, 102, 614-622

Navarrete S.A. & Berlow E.L. (2006) Variable interaction strengths stabilize marine community pattern. *Ecology Letters*, 9, 526-536

O'Hara R.B. (2005) The anarchist's guide to ecological theory. Or, we don't need no stinkin' laws. *Oikos*, 110, 390-393

Opitz S. (1996) *"Trophic interactions in caribbean coral reefs." Technical Report 43*. ICLARM, Manily.

Paine R.T. (1988) Food Webs – Road maps of interactions or grist for theoretical development. *Ecology*, 69, 1648-1654

Paine R.T. (1992) Food-web analysis through field measurement of per capita interaction strength. *Nature*, 355, 73-75

Polis G.A. (1991) Complex trophic interactions in deserts: an empirical critique of food-web theory. *American Naturalist*, 138, 123-155

Schmid-Araya J.M., Schmid P.E., Robertson A., Winterbottom J., Gjerløv C. & Hildrew A.G. (2002) Connectance in stream food webs. *Journal of Animal Ecology*, 71, 1056-1062

Schoener T.W. (1989) Food webs from the small to the Large. *Ecology*, 70, 1559-1589

Spencer M. & Warren P.H. (1996) The effects of habitat size and productivity on food web structure in small aquatic microcosms. *Oikos*, 75, 419-430

Stouffer D.B., Camacho J. & Amaral L.A.N. (2006) A robust measure of food web intervality. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 19015-19020

Stouffer D.B., Camacho J., Guimera R., Ng C.A. & Amaral L.A.N. (2005) Quantitative patterns in the structure of model and empirical food webs. *Ecology*, 86, 1301-1311

Tews J., Brose U., Grimm V., Tielborger K., Wichmann M.C., Schwager M. & Jeltsch F. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, 31, 79-92

Townsend C.R., Thompson R.M., McIntosh A.R., Kilroy C., Edwards E. & Scarsbrook M.R. (1998) Disturbance, resource supply, and food-web architecture in streams. *Ecology Letters*, 1, 200-209

Waide R.B. & Reagan W.B. (1996) *The food web of a tropical rainforest*. University of Chicago Press, Chicago.

Warren P.H. (1989) Spatial and Temporal Variation in the Structure of a Fresh-Water Food Web. *Oikos*, 55, 299-311

Williams R.J. & Martinez N.D. (2000) Simple rules yield complex food webs. *Nature*, 404, 180-183

Williams R.J., Martinez N.D., Berlow E.L., Dunne J.A. & Barabási A.-L. (2002) Two degrees of separation in complex food webs. *Proceedings of the National Academy of Science*, 99, 12913-12916

Winemiller K.O. (1990) Spatial And Temporal Variation In Tropical Fish Trophic Networks. *Ecological Monographs*, 60, 331-367

Woodward G. & Hildrew A.G. (2001) Invasion of a stream food web by a new top predator. *Journal of Animal Ecology*, 70, 273-288

Woodward G., Speirs D.C. & Hildrew A.G. (2005) Quantification and resolution of a complex, size-structured food web. In: *Advances In Ecological Research, Vol 36*, pp. 85-135

Wootton J.T. (1997) Estimates and tests of per-capita interaction strength: diet, abundance, and impact of intertidally-foraging birds. *Ecological Monographs*, 67, 45-64

Wootton J.T. & Emmerson M. (2005) Measurement of interaction strength in nature. *Annual Reviews Ecol. Evol. Systems*, 36, 419-444

Yodzis P. (1998) Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. *Journal of Animal Ecology*, 67, 635-658

Chapter 6

General Discussion

Endangered species. The photographs represent a selection of species of the *IUCN Red List* (clockwise): Blue Poison Frog *(Dendrobates azureus), Suriname; White*-headed Vulture (*Trigonoceps occipitalis*), Africa; Polar Bear (*Ursus maritimus*), Arctic; Angel Shark (Squatina squatina), Northeast Atlantic, Mediterranean and Black Seas and Giant Gartersnake (*Thamnophis gigas*), California, United States.

Photo credits: Russ Mittermeier, Nigel J. Dennis, Robert & Carolyn Buchanan, Simon Rogerson, Gary Nafis

The studies presented here demonstrate how the exploitation of natural ecosystems can lead to drastic changes in food-web structure, and thus affect ecosystem stability and functioning. Current anthropogenic disturbances of the natural environment across the globe include direct and well known environmental hazards such as the pollution and toxication of air and waterbodies, the reduction and fragmentation of wildlife habitats, overfishing and poaching as well as more subtle effects such as the introduction of invasive species. The consequences often lead to species loss, resulting in a drastic reorganization of many ecosystems. In some cases this may lead to the collapse of natural environments and their often underappreciated services to the human society (Daily *et al.* 1998). This scenario of massive species loss due to human influence is thus not hypothetical but a distressing fact, proofed each year by The World Conservation Union (IUCN). According to the 2007th Red List, each fourth mammalian species, eighth bird species, third amphibian species, fifth shark and ray species as well as 70% of all documented plant species are in danger of extinction. These facts address human responsibility to protect environment and to conduct fundamental research on ecological questions.

The main goal of ecology is to understand the interrelationships within natural ecosystems and to explain their functioning. Naturally, ecologists have to deal with very complex systems. Not only are the numbers of species and species' interactions tremendous, but they also depend on individual genetic dyes, spatial circumstances, physical and physiological attributes of the interacting species and on an environment that is full of influential biotic and a-biotic factors. This intrinsic complexity of ecosystems constrains ecologists to search for generalizations and patterns to be able to understand at least parts of ecosystem functioning and to scale them up to a greater context (MacArthur 1972, May 1986). Ecology has been pushed forward by new techniques in field research and the improved possibilities in theoretical modelling of complex systems. In particular, the computational simulation of complex food webs overcomes some limitations of field research, as these are restricted to either smaller sampling areas, simplified experiments or extended research periods to understand interactions and dynamics within ecosystems. A classic example is the 14-year sampling of the number of the apple-blossom thrips, *Thrips imaginis* (Bagnall), on flower butts in South Australia. Without originally intending to use this data as a basis for modelling, it was sampled and only later served as an inspiration for expressing and evaluating the underlying dynamics by a mathematical model (Davidson & Andrewartha 1948). Interesting on this example is that unexpected environmental conditions were found to be responsible for the complex abundance patterns of the thrips, which wasn't anticipated at first. This indicates the power of already earlier models and points out their contemporary importance.

Many field studies today, however, use modern experimental designs such as micro- or mesocosms to understand complex patterns and processes in species communities (Finke & Denno 2004, Petchey *et al.* 2004, Gamfeldt *et al.* 2005, Straub & Snyder 2006). The underlying simplified assumptions allow investigating more complex dynamics and species interactions than simple predator-prey pairs or food chains. However, they tolerate artificially assembled species communities within defined borders and are based on approximations of natural species' abundances. The study presented in Chapter 2 of this thesis tries to overcome such limitations, in extending the common approaches by investigating a small natural food web within its field habitat. This allowed for new insights in species dynamics and revealed interesting new parameters that have not been considered to be important before. For instance, the results of the study suggest that the natural phenology of the different predators in the food web plays a key role in explaining their different effects on prey and plant biomass. Moreover, predator-prey interaction strength was dependent not only on the interacting species, but also significantly affected by the identity of co-existing predators. A hidden interference between the different predators, implicitly documented because the study has been conducted under field conditions, might serve as a possible explanation for the observed behaviour. The study is thus amongst the first to show how important weak and indirect interactions between species are and it corroborates recent advances in food-web sampling and theoretical modelling, to take the relevance of link strength into account (McCann *et al.* 1998, Berlow 1999, Neutel *et al.* 2002, Navarrete & Berlow 2006). Crucial in this context is that the study simulated species loss by experimentally excluding predators from an intact small ecosystem. The results suggest that simple species traits of the excluded species, like their phenology, can have a profound impact on the remaining ecosystem. This concept was corroborated and expanded in a theoretical modelling project, described in Chapter 4 and discussed later here. The main limitation of the presented field study is that predator abundance in the field was not measured. This valuable information would have allowed for the calculation of predator biomass and per capita predator-prey interaction strengths and would have presumably revealed deeper insights on species dynamics (Berlow *et al.* 1999). Further, it would have been very important to involve climatic conditions in the data evaluation, as it turned out that the study was conducted in a year where beetle abundance was very high (2005). As an example, during 2007 hardly any beetle was detected at the investigated experimental sites, presumably due to extremely dry weather conditions during the preceding winter (Nathan Rank, personal communications). This fact leads to the request for a next logical step towards two different approaches: First, an extended field project could measure species abundances and climatic conditions over several years to understand

the complex dynamics and interrelationships between population size, species phenologies and environmental factors and allow predictions regarding climatic warming. It was already shown in other projects that extended and elaborate approaches can lead to interesting insights in complex species communities (Knapp & Matthews 2000, Knapp *et al.* 2001, Knapp *et al.* 2002). Second, the theoretical modelling of the studied food web, incorporating climatic records of the region, might reveal interesting and unexpected patterns and again allow predictions upon the future development of beetle and predator populations.

Theoretical modelling developed to become the most important tool to gain a general overview over complex systems and to uncover mechanisms that help to understand complex patterns and dynamics. The improvements of computational power of modern data processors allow dynamical investigations of increasingly large networks of interacting species. This development is accompanied by an enhanced possibility to include new and accurate parameters that describe natural conditions in greater detail. Beside the consideration of link strength, one of the most important recent advances in theoretical ecology was the sampling and consideration of species' body masses. These and the body-mass ratios between consumers and resources are increasingly recognized to have a profound impact on ecosystem stability and functioning in both theoretical and applied analyses (Emmerson *et al.* 2005, Loeuille & Loreau 2005, Brose *et al.* 2006, Neutel *et al.* 2007). In Chapter 3 in this thesis we use this finding and a bioenergetic consumer-resource model (Yodzis & Innes 1992) to simulate tri-trophic food chains and 20-species food webs under varying body mass-ratios between the species. Our results reveal an energetically driven mechanistic basis of body-mass effects on population persistence in both food chains and complex food webs. We suggest that empirical allometric degree distributions in which larger species feed on more prey and are consumed by fewer predators than small species across five natural food webs may explain how these distributions affect population persistence and food-web stability in natural communities. Randomized re-wiring analyses of the empirical data revealed that the empirical body-mass distribution within the natural food webs, which evolved during a very long time, was already sufficient to explain 81% of the investigated food-web stability. Empirical body-masses lead to empirical food-web structures and together these two variables explained 94.7% stability. These results highlight the importance of species' body masses for food-web stability and manifest the importance of food-web structure as an important network of energetic pathways between the species. In conclusion, our findings reveal for the first time the connection between species' body masses and network structure, and will certainly influence further analyses regarding food-web structure. We highlight that food-web stability is not necessarily dependent on network size but primarily on the energetic

fluxes between the species within the food webs. Moreover the study emphasizes yet again that food-web patterns are not random but developed evolutionary over a long time. However, future extensions of our approach need to also address a higher degree of variation between network motifs, network size and metabolic types of species to confirm the generality of the described results.

Chapter 4 of this thesis combines the implications of species loss on the remaining ecosystem and the modelling of complex food-web dynamics under the consideration of species' body masses. The study emphasises that the loss of a species alters the structure of the remaining system considerably, resulting in a decreasing food-web robustness against cascading secondary extinctions. We find that food-web robustness is primarily dependent on species diversity and the number of basal species within nine tested empirical food webs. This may be explained by the fact that a higher number of basal species increases the overall bottom-up energy availability and the structural redundancy of multiple energetic pathways in food webs (see prior model studies, e.g., Borrvall *et al.* 2000, Ebenman *et al.* 2004, Thébault *et al.* 2007), providing insurance against secondary extinctions. Interestingly, the major effect strength of basal species diversity reveals the importance of a very simple characteristic of complex natural food webs that have not been considered in prior studies. This is astonishing and the strong effects were virtually to be expected, as basal species are commonly known to serve as the main energy resource in most if not all natural ecosystems. Thus, our novel results encourage a focus on simple and basic characteristics in order to understand causal relationships in complex systems. The same perspective is valid when analysing the characteristics of the species that were initially excluded from the studied food webs. Food-web robustness was primarily dependent on the body masses of the initially lost species. Hence, the study again corroborates the common perception of the importance of species' body masses to significantly affect food-web stability and is in line with recent analyses on food-web stability (Emmerson *et al.* 2004, Brose *et al.* 2006). A major advancement of this study compared to prior analyses is the combination of structural and dynamical investigations of a large contemporary data set of natural food-webs. However, the deficits of the available data still restricted our analyses to relatively small food webs (up to 116 species). Future improvements of data will hopefully allow for even more complex and accurate simulations and give more detailed insights on how species loss might affect natural ecosystems.

The studies in Chapters 2 to 4 use different approaches to investigate the implications of species loss on food-web structure while Chapters 3 and 4 demonstrate the importance of food-web structure *per se* on ecosystem stability. It is thus an appropriate add-on to this thesis to include a review study on link density and

connectance within food webs, as these are two important measures of bio-complexity and known parameters to affect food-web stability (Chapter 5). Both parameters describe the interlinking between the species (i.e., the number of links per species and the fraction of realized links in a network, respectively) and thus measure the realized amount of energetic pathways within food webs, indirectly pointing out the relevance of energetic reallocation structures for food-web stability. The study investigates most recent food-web data, and shows that both parameters, link density and connectance, are most likely to be scale-dependent, which revisits, and possibly ends, a long lasting debate whether or not these two parameters scale with food-web diversity. We found that link density significantly increases with species diversity whereas connectance decreases. This supports the finding that destabilizing effects of increasing diversity need to be balanced by a decrease in connectance to avoid instability (Montoya & Solé 2003). This argument mechanistically links variation in species diversity, community complexity and energetic balance in ecosystems. Worked examples on 14 further parameters of food-web topology showed either significant scale-dependence (in case of six variables), or high coefficients of variation that imply the non-constancy of the remaining variables. Such, the study finds the quest for general and scale-independent laws in natural ecosystems as ended with the result that they most likely do not exist. This illustrates the tremendous dynamics within living ecosystems that are dependent on an overwhelming number of intrinsic and extrinsic factors that do naturally not allow for common laws. However, interestingly the study found the majority of the analysed topology parameters to exhibit saturating trends with very high levels of species richness. This indicates that at least diverse communities, such as most natural ecosystems, could be characterized by scale-independent constant food-web parameters. This again supports the demand for the compilation of new food-web data of large networks to refine the so far achieved findings.

Perspectives

The theoretical simulation approach used in the presented studies is based on several simplifying assumptions that might be possibly resolved by future research attempts.

First, the currently used food-web data ignores sampling errors and population fluctuations over time. Important are not only annual fluctuations, presumably derived from different climatic conditions, but also seasonal variations in species composition, which are either not captured or possibly mixed up, when the sampling of data lasts several months or years. New food-web data could consider this and provide on one

hand seasonal versions of the feeding communities and on the other hand climatic and temperature information of the different sampling periods. Additionally, it would be a promising simulation approach to include climatic data, sampled from weather stations from all over the globe, in ecosystem modelling and to investigate effects of changing climatic conditions on the dynamics and population persistence in food webs.

Second, body masses of the species vary considerably among and within populations, particularly if immature and adult individuals are considered. This has an important impact on energetic principles within the populations that is neglected in results generalized from the assumption of homogeneous populations of adult individuals. Essential in this context is the often ignored different diet of immature and adult individuals, primarily in aquatic systems. However, new and modern food webs like the Weddell Sea Shelf food web overcome these limitations. Being one of the currently best sampled and largest food webs available, the Weddell Sea food web provides a unique species resolution (i.e., no trophic species) and accurately measured body-mass data of all species, contrasting many literature-based estimates for most other available food webs. It further distinguishes between larval and mature stages of the described species and thus fulfils the demands for improved food-web data. Unfortunately, the desired direct measurement of quantitative link strength is missing here as well. This dimension of food-web data still is and will remain a very difficult task to gather. Nevertheless, the data is leading in terms of high food-web quality and may hopefully serve as an example for further sampling approaches.

Third, species habitats are often considered to be bounded (e.g., "Skipwith Pond", "Coachella Dessert" or "Benguela Bay"), and thereby classified either aquatic or terrestrial, either aboveground or belowground. However, natural ecosystems overlap, interact and are linked with each other by energy fluxes and individual dispersal across habitat boundaries. Examples are hunting spiders that connect above- and belowground systems (Scheu 2001), or dragonflies, which spend parts of their life in aquatic and parts in terrestrial systems. In this context it was shown that the feeding of fish on dragonfly larvae facilitates terrestrial plant reproduction, as a reduced population of adult dragonflies leads to decreased predation on plant pollinating insects (Knight *et al.* 2005). Further overlap at the aquatic-terrestrial interface exists, where terrestrial species may hunt on aquatic prey or where terrestrial detritus supplies aquatic ecosystems. Spatial patterns in landscapes and the dispersal of species between different habitats are very common in natural environments, but considered only in few ecological studies (e.g., Levin 1992, Hastings 1993, Jackson 1994, Holt & McPeek 1996, Cowen *et al.* 2000, Loreau *et al.* 2003, Brose *et al.* 2005, Koelle & Vandermeer 2005). Further extensions in simulations might be able to include the

interlinking of different ecosystem types and provide new and interesting dynamics and patterns that increase the current understanding of ecosystem processes.

Finally, the calculated consumer-resource interactions in the applied simulations were restricted to predator-prey relations but ignored parasitic or parasitoid-host interactions. This was necessary, as parasite-host interactions follow different bioenergetic principles than predator-prey dynamics and exhibit different body-mass ratios between the trophic higher and lower species than in predator-prey pairs (thus, parasites and parasitoids are smaller than their hosts; e.g., Cohen *et al.* 2005). Future models that included parasite-host relationships beside common consumer-resource interactions could provide amazingly new insights in integrated whole-ecosystem functioning with novel energetic fluxes and resultant population dynamics beyond the common perception.

References

Berlow E.L. (1999) Strong effects of weak interactions in ecological communities. *Nature*, 398, 330-334

Berlow E.L., Navarrete S.A., Briggs C.J., Power M.E. & Menge B.A. (1999) Quantifying variation in the strengths of species interactions. *Ecology*, 80, 2206-2224

Borrvall C., Ebenman B. & Jonsson T. (2000) Biodiversity lessens the risk of cascading extinction in model food webs. *Ecology Letters*, 3, 131-136

Brose U. (2005) Spatial aspects of food webs. *In: Dynamic Food Webs: Multispecies assemblages, ecosystem development, and environmental change* (eds. De Ruiter P, Moore JC & Wolters V). Elsevier/Academic Press, San Diego, CA

Brose U., Williams R.J. & Martinez N.D. (2006) Allometric scaling enhances stability in complex food webs. *Ecology Letters*, 9, 1228-1236

Cohen J.E., Jonsson T., Müller C.B., Godfray H.C.J. & Savage V.M. (2005) Body sizes of hosts and parasitoids in individual feeding relationships. *Proceedings of the National Academy of Science of the United States of America*, 102, 684-689

Cowen R.K., Lwiza K.M.M., Sponaugle S., Paris C.B. & Olson D.B. (2000) Connectivity of marine populations: open or closed? *Science*, 287, 857-859

Daily G., Dasgupta P., Bolin B., Crosson P., du Guerny J., Ehrlich P., Folke C., Mansson A.M., Jansson B.O., Kautsky N., Kinzig A., Levin S., Müller K.G., Pinstrup-Anderson P., Siniscalco D. & Walker B. (1998) Food production, population growth, and the environment. *Science*, 281, 1291-1292

Davidson J. & Andrewartha H.G. (1948) The Influence of Rainfall, Evaporation and Atmospheric Temperature on Fluctuations in the Size of a Natural Population of *Thrips imaginis*. *Journal Of Animal Ecology*, 17, 200-222

Ebenman B., Law R. & Borrvall C. (2004) Community viability analysis: The response of ecological communities to species loss. *Ecology*, 85, 2591-2600

Emmerson M., Bezemer T.M., Hunter M.D., Jones T.H., Masters G.J. & Van Dam N.M. (2004) How does global change affect the strength of trophic interactions? *Basic And Applied Ecology*, 5, 505-514

Emmerson M., Montoya J.M. & Woodward G. (2005) Body size, interaction strength, and food web dynamics. *In: Dynamic Food Webs: Multispecies assemblages, ecosystem development, and environmental change* (eds. De Ruiter P, Moore JC & Wolters V), pp. 167-178. Elsevier/Academic Press, San Diego, CA

Finke D.L. & Denno R.F. (2004) Predator diversity dampens trophic cascades. *Nature*, 429, 407-410

Gamfeldt L., Hillebrand H. & Jonsson P.R. (2005) Species richness changes across two trophic levels simultaneously affects prey and consumer biomass. *Ecology Letters*, 8, 696-703

Hastings A. (1993) Complex interactions between dispersal and dynamics: lessons from coupled logistic equations. *Ecology*, 74, 1362-1372

Holt R.D. & McPeek M.A. (1996) Chaotic population dynamics favors the evolution of dispersal. *American Naturalist*, 148, 709-718

Jackson J.B.C. (1994) Community unity? *Science*, 264, 1412-1413

Knapp A.K., Fay P.A., Blair J.M., Collins S.L., Smith M.D., Carlisle J.D., Harper C.W., Danner B.T., Lett M.S. & McCarron J.K. (2002) Rainfall Variability, Carbon Cycling, and Plant Species Diversity in a Mesic Grassland. *Science*, 298, 2202-2205

Knapp R.A. & Matthews K.R. (2000) Non-native fish introductions and the decline of the mountain yellow-legged frog from within protected areas. *Conservation Biology*, 14, 428-438

Knapp R.A., Matthews K.R. & Sarnelle O. (2001) Resistance and resilience of alpine lake fauna to fish introductions. *Ecological Monographs*, 71, 401-421

Knight T.M., McCoy M.W., Chase J.M., McCoy K.A. & Holt R.D. (2005) Trophic cascades across ecosystems. *Nature*, 437, 880-883

Koelle K. & Vandermeer J. (2005) Dispersal-induced desynchronization: from metapopulations to metacommunities. *Ecology Letters*, 8, 167-175

Levin S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, 73, 1943-1967

Loeuille N. & Loreau M. (2005) Evolutionary emergence of size-structured food webs. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 5761-5766

Loreau M., Mouquet N. & Gonzalez A. (2003) Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 12765-12770

MacArthur R.H. (1972) *Geographical ecology: Patterns in the distribution of species.* Harper and Roy, New York.

May R.M. (1986) The search for patterns in the balance of nature: advances and retreats. *Ecology*, 66, 1115-1126

McCann K., Hastings A. & Huxel G.R. (1998) Weak trophic interactions and the balance of nature. *Nature*, 395, 794-798

Montoya J.M. & Solé R.V. (2003) Topological properties of food webs: from real data to community assembly models. *Oikos*, 102, 614-622

Navarrete S.A. & Berlow E.L. (2006) Variable interaction strengths stabilize marine community pattern. *Ecology Letters*, 9, 526-536

Neutel A.-M., Heesterbeek J.A.P. & De Ruiter P.C. (2002) Stability in real food webs: weak links in long loops. *Science*, 296, 1120-1123

Neutel A.M., Heesterbeek J.A.P., van de Koppel J., Hoenderboom G., Vos A., Kaldeway C., Berendse F. & de Ruiter P.C. (2007) Reconciling complexity with stability in naturally assembling food webs. *Nature*, 449, 599-602

Petchey O.L., Downing A.L., Mittelbach G.G., Persson L., Steiner C.F., Warren P.H. & Woodward G. (2004) Species loss and the structure and functioning of multitrophic aquatic systems. *Oikos*, 104, 467-478

Scheu S. (2001) Plants and generalist predators as links between the below-ground and above-ground system. *Basic And Applied Ecology*, 2, 3-13

Straub C.S. & Snyder W.E. (2006) Species identity dominates the relationship between predator biodiversity and herbivore suppression. *Ecology*, 87, 277-282

Thébault E., Huber V. & Loreau M. (2007) Cascading extinctions and ecosystem functioning: contrasting effects of diversity depending on food web structure. *Oikos*, 116, 163-173

Yodzis P. & Innes S. (1992) Body size and consumer-resource dynamics. *American Naturalist*, 139, 1151-1175

Summary

Understanding the structure and dynamics of ecological networks is critical for understanding the persistence, stability and functioning of ecosystems. The studies presented here investigate the stability of natural ecosystems, either in response to perturbations such as species loss or under the consideration of structural implications.

In a field survey that spanned an entire reproductive season of a simple montane food web (Chapter 2), I was experimentally excluding the predators of the herbivorous beetle *Chrysomela aeneicollis*. This perturbation altered the structure of the studied food web and simulated species loss at higher trophic levels, which allowed monitoring of cascading effects via two trophic levels within the food web. High predator diversity suppressed herbivores and consequently released plants from top-down pressure. With a full-factorial design of predator removal, I could distinguish between the effects of diversity loss due to both additive effects of predators and predator compensation. Interestingly, pair-wise predator-prey interaction strengths and larval survivorship of the beetles over time varied with predator diversity and the identity of co-existing predators. Variation in predator diversity effects is explained by predator phenology and modified food-web structure.

Besides this project based on field research, I employed also theoretical model simulations to understand complex dependencies within food webs (Chapter 3). In line with recent theoretical advances I applied a bioenergetic dynamically consumer-resource model to present a mechanistic explanation for why predator-prey body-mass ratios may be critically important for complex food-web stability. Simulations show that only certain combinations of body-mass ratios between three species in a food chain allow their stable co-existence. The resultantly defined 'stability domain' is restricted by bottom-up energy availability towards low and enrichment-driven dynamics towards high body-mass ratios. Consistent with the model predictions, more than 97% of three-species food chains across five natural food webs exhibit body-mass ratios within this 'stability domain'. Random re-wiring analyses of the food webs demonstrate that allometric link-degree distributions in natural food webs are critically important for this consistency. They hold that the numbers of predators per species decreases whereas the number of prey per species increases with species' body masses. Food-web stability emerges from these simple allometric link-degree distributions that are caused by physical constraints on predator-prey interactions. The study demonstrates how simple, species-level correlations between body-masses and linking drive community-level processes such as food-web stability.

This food-web stability, however, is critically dependent on species loss. In a subsequent project (Chapter 4) I also applied a bioenergetic model approach to simulate species loss on a data set derived from nine empirically sampled food webs. Food-web response to species removal was measured depending on five topological food-web parameters such as diversity and the number of basal species, and five species traits, such as the body masses of the species removed and three parameters that describe their the characteristics of their network environment. Contributing to a recent discussion about the implications of species loss, the removal simulations were conducted under two opposing assumptions of predator interference and non-interference. Interestingly, the study revealed similar results under both conditions. The robustness of ecological networks after species loss is negatively related with network diversity and the average level of omnivory, but positively correlated with the number of basal species in the networks and the average trophic level. On the species level, food-web robustness was higher when the species initially removed had small body sizes, high trophic levels and low generality. This suggests that the loss of large, generalist consumer species at low trophic levels in diverse food webs with few basal species are most likely to trigger cascades of secondary extinctions within ecological communities. These results enable interesting predictions on the consequences of species loss on ecosystem functioning.

Studying on the consequences of species loss leads back to the question on the persistence and stability of ecosystems and therewith to food-web topology *per se*. The relationship between the diversity and topology of food webs is debated since a long time. Early models assumed the number of links per species to be constant, i.e., scale independent, resulting in a decreasing connectance with increasing species number. However, other studies on new data showed these assumptions to be unrealistic and claimed "constant connectance" in food webs. In Chapter 5 of this thesis, we analyze existing relationships between diversity and complexity of natural food webs and discuss explanations for the meanwhile more broadly accepted scale dependence of complexity. We hypothesise that for example a decrease in connectance with increasing food-web complexity may be reasoned due to the difficulty to find weak links in larger systems, resulting in an assumed less efficient sampling in lager webs in contrast to smaller ones. Further, an increase in habitat complexity might be dependent on an increase of specific sub-habitats, where predator and possible prey species are less likely to interact. Meta-communities may cross habitat boundaries, which may explain an increase in species diversity in total, but lead to decreased connectance due to decreased overlap of populations. Additional to the reviewing and discussion of possible mechanisms on scale dependence of complexity, the study includes own data analyses on one of the largest and best sampled empirical

data sets available. These analyses reinvestigate common measures of bio-complexity (e.g., the fractions of top, intermediate and basal species or the average levels of omnivory and trophic level of species within the food webs) and found a scale dependent behaviour of most food-web properties. Interestingly, the functions of food-web parameters on diversity show saturation at very high diversity levels. These new results give an intriguing overview on the common state-of-the-art perception on the scale dependency, or better, scale in-dependency of structural food-web parameters on ecosystem diversity.

Together, the experimental and theoretical work presented here contributes on the understanding on the dynamical processes between interacting species in ecosystems. It shows how energy fluxes can affect the stability of natural communities, how simple structural aspects can influence the interplay between entire populations and how different attributes of the species – or of the communities – are interrelated and dependent on each other.

Zusammenfassung

Die Analyse von Struktur und Dynamik in ökologischen Netzwerken ist von besonderer Bedeutung für das Verständnis der Persistenz und Stabilität von Ökosystemen und ihrer Funktion. Die hier vorgelegten Studien untersuchen die Stabilität von natürlichen Ökosystemen, entweder in Abhängigkeit von Störungen wie zum Beispiel dem Verlust von Arten oder im Zusammenhang mit Veränderungen in der Netzwerk-Struktur.

In einem Feldexperiment in den kalifornischen Sierra Nevadas, USA, habe ich ein einfaches Nahrungsnetz während einer gesamten Entwicklungsperiode untersucht (Kapitel 2). Dabei schloss ich experimentell drei verschiedene Räuber eines herbivoren Käfers, *Chrysomela aeneicollis*, einzeln oder in Gruppen aus dem Netzwerk aus, um die Effekte des simulierten Artenverlustes auf den Käfer und die Pflanzenbiomasse zu bestimmen. Wie erwartet dezimierte eine größere Vielfalt von Räubern die Anzahl der Herbivoren merklich, so dass sich der Fraßdruck auf die Pflanze messbar verringerte. Durch den Ausschluss der Räuber in verschiedenen Kombinationen konnte ich sowohl additive Effekte feststellen, bei denen die Wirkung von mehreren Räubern deutlich größer war als die von wenigeren, als auch kompensatorische, bei denen der Verlust eines Räubers durch die Anwesenheit der verbleibenden ausgeglichen wurde. Die Interaktionsstärke zwischen Räuber und Beute wie auch die Überlebens-wahrscheinlichkeit der Käferlarven als hauptsächliche Beute im Laufe der Entwicklungsperiode war von der Anzahl und Identität der gemeinsam vorkommenden Räuber abhängig. Die Streuung der Ergebnisse der Identitätseffekte kann durch die unterschiedliche Phänologie der Räuber und die durch Artenausschluss veränderte Netzwerkstruktur erklärt werden.

Neben der empirischen Feldarbeit untersuchte ich komplexe Zusammenhänge in Nahrungsnetzen vor allem über die computerbasierte theoretische Modellierung. Im Einklang mit kürzlich durchgeführten theoretischen Untersuchungen, habe ich in Kapitel 3 ein bioenergetisch-dynamisches Räuber-Beute-Model angewendet, um eine mechanistische Erklärung für die Bedeutung von Körpergrößen-Verhältnissen zwischen Räuber und Beute für die Stabilität gesamter natürlicher Netzwerke zu finden. Die Simulationen von Drei-Arten-Ketten zeigten, dass nur bestimmte Körpergrößen-Kombinationen zwischen Räuber und Beute eine stabile Koexistenz von drei Arten zuließen, die durch eine "Stability Domain" abgebildet werden konnten. Dies war einerseits auf eine energetische Limitierung der Top-Räuber zurückzuführen, wenn kleine Körpergrößen-Verhältnisse simuliert wurden, sowie andererseits auf übersteuernde Biomasse-Oszillationen der intermediären Arten der Ketten aufgrund

einer Anreicherung von Nährstoffen bei Simulationen großer Körpergrößen-Verhältnisse. In Übereinstimmung mit den Modell-Vorhersagen zeigten über 97% der tatsächlich vorkommenden Drei-Arten-Ketten in fünf verschiedenen empirischen Nahrungsnetzen Körpergrößen-Verhältnisse, die innerhalb der simulierten "Stability Domain" lagen. Dies konnte durch die Anwendung von Randomisierungs-Prozessen, welche die empirischen Netzwerkstrukturen veränderten, erklärt werden. Auf der Basis dieser Prozesse ließ sich nachweisen, dass die körpergrößenabhängige Verteilung der lokalen Vernetzung der Arten für die empirische Netzwerkstabilität verantwortlich ist. So konnten wir zeigen, dass größere Arten deutlich mehr Beute-Arten und dabei deutlich weniger Räuber-Arten haben als kleine. Dieser Zusammenhang impliziert die oben beschriebenen physikalisch-energetischen Randbedingungen für die Arten. Die Studie zeigt, wie sich der Zusammenhang zwischen der Körpergröße und der lokalen Vernetzung der Arten in einem Ökosystem auf die Stabilität der gesamten Artengemeinschaft auswirken kann.

Zusätzlich zur Körpergröße der Arten sind weitere Faktoren innerhalb und außerhalb von Ökosystemen für deren Existenz und Stabilität verantwortlich. Unter der Anwendung eines weiteren bioenergetisch-dynamischen Simulationsmodells untersuchte ich in Kapitel 4 die Auswirkung von Artenverlust auf neun verschiedene empirische Ökosysteme. Die Robustheit der Nahrungsnetze gegen sekundäre Aussterbeereignisse wurde an fünf topologischen Kenngrößen der Netzwerke evaluiert, wie zum Beispiel deren Artenvielfalt oder der Anzahl ihrer Basalarten, sowie an fünf Eigenschaften der ausgeschlossenen Arten, wie ihre Körpergröße und drei Kenngrößen, die ihre lokale Verlinkung beschreiben. Der Ausschluss der einzelnen Arten wurde unter zwei aktuell diskutierten Grundannahmen simuliert, zum einen unter der Annahme, dass sich die Arten innerhalb einer Population gegenseitig beeinflussen und zum anderen ohne Interferenz. Interessanterweise waren die Ergebnisse der Studie, im Gegensatz zu der laufenden Diskussion, unter beiden Annahmen sehr ähnlich. So sind besonders kleine ökologische Netzwerke mit einem hohen Anteil an Basalarten robust, wenn sie geringe durchschnittliche Omnivorie und einen im Durchschnitt hohen trophischen Grad der Arten aufzeigen. Hinsichtlich der Charaktereigenschaften der ausgeschlossenen Arten wirken sich kleine Körpergrößen, ein niedriger trophischer Grad und ein hoher Spezialisierungsgrad positiv auf die Robustheit von Nahrungsnetzen aus. Auf der Basis dieser Studie können wichtige Voraussagen zu den Auswirkungen von Artensterben auf Ökosysteme und deren Funktion und Stabilität getroffen werden.

Grundsätzlich hat also vor allem die Struktur von Nahrungsnetzen eine große Bedeutung für deren Stabilität. Der Zusammenhang zwischen der Artenvielfalt und der

Topologie von Netzwerken wird in der Ökologie seit langem angeregt diskutiert. Frühere Modelle erkannten keinen Zusammenhang zwischen der Anzahl der Verbindungen einer Art zur anderen und der Größe der Netzwerke, so dass die lokale Verlinkung als skalenunabhängig erklärt wurde. Dies beinhaltet einen sinkenden durchschnittlichen Vernetzungsgrad der Nahrungsnetze mit steigender Artenvielfalt. Neuere Studien, die auf einer Vielzahl von neu erfassten Nahrungsnetzen basieren, widersprachen den früheren Resultaten und postulierten einen skalenunabhängigen Vernetzungsgrad von Nahrungsnetzen. Kapitel 5 dieser Arbeit fasst die Diskussion über diese beiden Standpunkte zusammen und diskutiert mögliche Erklärungen für die gefundenen Muster. So ist zum Beispiel ein sinkender Vernetzungsgrad mit zunehmender Artenvielfalt nachvollziehbar, wenn man davon ausgeht, dass das Erfassen von sehr schwachen oder raren Interaktionen zwischen zwei Arten wesentlich schwieriger wird, je mehr Arten zu beobachten sind. Weiterhin könnte ein größerer Lebensraum in viele kleine, voneinander abgetrennte, Habitate unterteilt sein, wodurch das Zusammentreffen von möglichen Räuber- und Beutearten erschwert würde und einen reduzierten Vernetzungsgrad zur Folge hätte. Zusätzlich zu der Revision der Meinungen über den Vernetzungsgrad und der Diskussion seiner möglichen Mechanismen, präsentiert die Arbeit eigene Analysen an dem bislang größten und modernsten Datensatz an Nahrungsnetzen. In diesen Analysen wurden noch einmal die Zusammenhänge zwischen herkömmlichen Parametern der Bio-Komplexität (wie zum Beispiel der Anteil von Arten ohne Räuber, mit Räubern und Beute, oder Basalarten in den Netzwerken) mit der Artenvielfalt untersucht. Die Erhebungen zeigen, dass die meisten Parameter zwar deutlich mit der Artenvielfalt korrelieren, aber eine Sättigung bei sehr großen Nahrungsnetzen aufweisen. Diese neuen Ergebnisse verbinden die bislang widersprüchlichen Meinungen und geben einen ausführlichen Überblick über das Verhalten von herkömmlichen Netzwerkparametern in Abhängigkeit von der Artenvielfalt in natürlichen Nahrungsnetzen.

Zusammenfassend, tragen die hier vorgestellten Arbeiten dazu bei einen tieferen Einblick in die dynamischen Prozesse zwischen interagierenden Arten in Nahrungsnetzen zu erlangen. Die Ergebnisse zeigen, wie der Austausch von lebenswichtigen Energien zwischen den Arten die Stabilität des gesamten Netzwerkes beeinflussen kann, wie einfache strukturelle Parameter das Zusammenspiel zwischen verschiedenen Populationen beeinflussen können und wie die Eigenschaften von Arten oder Nahrungsnetzen miteinander verknüpft sind und sich gegenseitig beeinflussen.

Acknowledgements (Danksagungen)

And here comes the worst part to write – how to thank all of you in an appropriate way, without forgetting those who expect themselves to be certainly mentioned or without listing you in a wrong order. Let me try it this way...

First of all, my deep thanks to Uli Brose, who lead me through all this with never ending patience, knowledge and esprit. Without you, this thesis and its publications would have been not possible and I am honoured to have you as my PhD supervisor. Thanks for not letting me go, when I cancelled my job yet again...

As for the other people I had the chance to meet: I was often stunned about the different kinds of support, wisdom and friendship I encountered during my work. This certainly includes the collaborators of the different projects of this thesis but also involves the frequent other friendly encouragements from various other sides. It also never happened to me that questions I had remained unanswered. I am very grateful to many of you (and you know, so please read your name between these lines!).

Together with a wonderful and cooperative workgroup, who supported me even when I was difficult, who made me laugh many times and who edited grand parts of my work, I enjoyed my time as PhD-student in the EcoNetLab a lot. Thanks for that!

The rest goes to my family, to Oli, my friends and climbing partners:

Dank' an Euch, die Ihr immer neugierig, aufmunternd und wohlwollend seid. Euer Interesse an meinem Tun, aber auch die erfrischende Ablenkung die Ihr mir immer wieder bereitet, sind mir gleichermaßen wichtig und haben sicherlich auch zum Gelingen dieser Arbeit beigetragen.

Danke aber vor allem an Mutzi und Papa, die Ihr wieder einmal gezeigt habt, dass Ihr meine Sperenzchen unterstützt und letztendlich gutheißt. Das ist mir sehr wichtig.

Curriculum vitae

Name	Sonja B. Otto
Date of Birth	21. September 1974
Place of Birth	Nürnberg, Germany
Family status	unmarried

Professional and Scientific Career

10/2004-04/2008 **Technical University of Darmstadt**

Dissertation in Ecology and ecological modelling
Supervisor: Dr. Ulrich Brose, EcoNetLab

04/2003-07/2004 **University of Cologne**

Postgraduate course in Bioinformatics (CUBIC) and subsequent employment at the apartment of Bioinformatics

10/1996-03/2003 **University of Regensburg**

Diploma in Biology (Zoology, Botany and History of Science)

09/1994-10/1996 **uniVersa a.G., Nürnberg**

Apprenticeship and employment as insurance agent

09/1981-07/1994 **Primary and Grammar School in Stein**

Degree: Baccalaureate

Grants and Scholarships

04/2003-04/2004 Scholarship of the **Federal Ministry of Science**

10/2007-02/2008 Scholarship of the **Fazit Foundation**

List of publications and talks

Publications

Otto, S.B., Rall, B.C. & Brose, U. (2007). Allometric degree distributions facilitate food web stability. *Nature* (450) 1226-1229.

Otto, S.B., Berlow, E.L., Rank, N.E., Smiley, J. & Brose, U. (2008). The diversity and identity of predators drive interaction strengths and trophic cascades in a montane food web. *Ecology* (89) 1.

Otto, S.B., Martinez, N.D. & Brose, U. (2008). Body mass and network structure drive food-web robustness against secondary extinctions (submitted).

Brose, U., Banašek-Richter, C., **Otto, S.B.**, Rall, B.C. & Dunne, J. (2008). The complexity, topology and diversity of complex food webs (submitted).

Talks

36. Annual Meeting of the Ecological Society of Germany, Austria and Switzerland (GfÖ), Bremen, Germany, September 2006. Symposium "Multitrophic Interactions": Predator diversity drives pair-wise interaction strength and trophic cascades in a natural food web.

Workshop LEM II – "Theories of Species Richness", Yasinya, Ukraine, February 2007: The influence of body size on species richness.

92. ESA/SER Joint Meeting, San José, Kalifornien, USA, August 2007. Symposium "Ecological concepts and processes": Food-web stability emerges from allometric link-degree relationships.

37. Annual Meeting of the Ecological Society of Germany, Austria and Switzerland (GfÖ), Marburg an der Lahn, Germany, September 2007. Symposium "Multitrophic Interactions": Food-web stability emerges from allometric link-degree relationships.

Eidesstattliche Erklärung

Ich erkläre hiermit an Eides statt, dass ich die vorliegende Dissertation selbstständig und nur mit den angegebenen Hilfsmitteln angefertigt habe. Die analytischen Berechnungen zu Iso-Oberflächen von Drei-Arten Ketten in Kapitel 3 wurden vorwiegend von meinem Co-Autor Björn C. Rall durchgeführt.
Ich habe noch keinen Promotionsversuch unternommen.

Darmstadt, den 25. Januar 2008

Sonja Otto